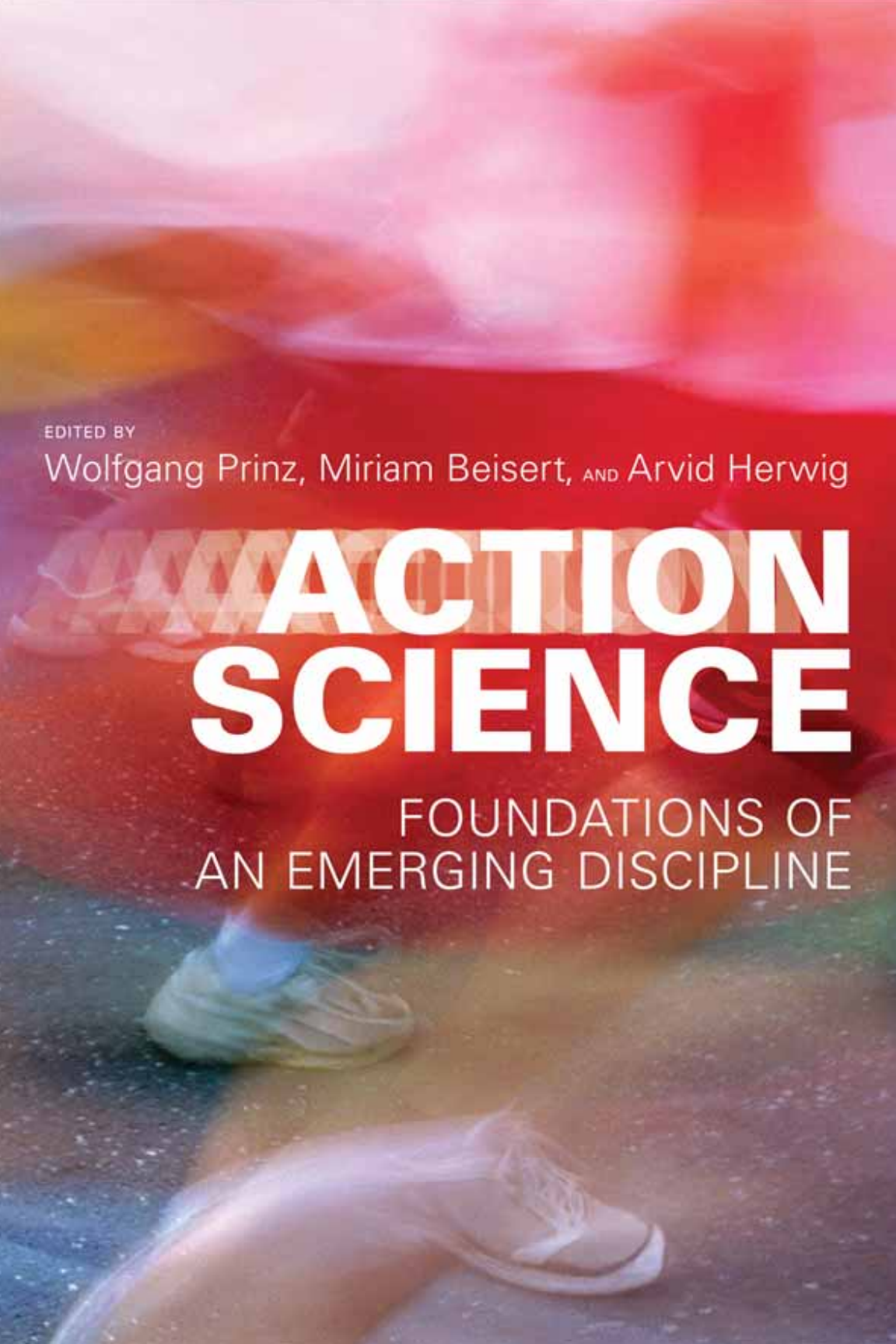
EDITED BY
Wolfgang Prinz, Miriam Beisert, AND Arvid Herwig
ACTION SCIENCE
FOUNDATIONS OF AN EMERGING DISCIPLINE

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Foundations of an Emerging Discipline

edited by Wolfgang Prinz, Miriam Beisert, and Arvid Herwig

The MIT Press
Cambridge, Massachusetts
London, England

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This book was set in Stone Sans and Stone Serif by Toppan Best-set Premedia Limited, Hong Kong. Printed and bound in the United States of America.

Library of Congress Cataloging-in-Publication Data

Action science : foundations of an emerging discipline / edited by
Wolfgang Prinz, Miriam Beisert, and Arvid Herwig.
p.cm.
Includes bibliographical references and index.
ISBN 978-0-262-01855-5 (hardcover : alk. paper)
1. Motivation (Psychology). 2. Cognitive psychology. I. Prinz, Wolfgang, 1942–. II. Beisert, Miriam, 1980–. III. Herwig, Arvid, 1979–.
BF503.A28 2013
153—dc23
2012024586

10 9 8 7 6 5 4 3 2 1

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Acknowledgments

We are indebted to the chapter contributors and to all who helped editing the book by reviewing the contributions. The majority of chapters originate from papers presented at the conference "Perception and Action," held in June 2010 at the Center for Interdisciplinary Research (ZiF) at Bielefeld University. "Perception and action" is a topic that was first examined at ZiF in the study year 1984–85, a quarter century ago. A few chapters were written later to complete the picture. The conference was made possible by the generous support of the Center for Interdisciplinary Research (ZiF). We also acknowledge the financial support of the German Research Foundation (DFG), the Leibniz Research Centre for Working Environment and Human Factors, and the Max Planck Institute for Human Cognitive and Brain Sciences. We would also like to thank Herbert Heuer and Peter Wolff for organizing the conference together with us, as well as the staff at ZiF for their warm hospitality. Moreover, we owe special thanks to Philip Laughlin and Judy Feldmann at MIT Press for guiding the process with the utmost competence and care. Finally, we would like to thank our colleagues, friends, and families for their support while we worked on this volume.

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1 Action Science Emerging: Introduction and Leitmotifs

Arvid Herwig, Miriam Beisert, and Wolfgang Prinz

Introduction

Our ability to interact with the environment can be considered an essential aspect of our waking life. All day long we engage in a vast number of actions like turning off the alarm clock, getting out of bed, dressing, eating breakfast, reading the newspaper, going to work, meeting friends, and ending the day by setting the alarm clock again. Actions stimulate our mental life and help us to structure our day. Above all, actions are indispensable to the survival of humankind. Without actions, we could not obtain food, we could not brave the elements, and we could not reproduce. Only by means of our actions are we capable of attaining our goals and accommodating environmental demands in ever-changing situations. Thus, seen from an evolutionary perspective, actions have direct implications for an agent's fitness. One might even assert that our brains and minds have evolved to serve the demands of smart action rather than of true cognition (Llinás, 2001).

Despite its eminent status, both in everyday life and in the evolution of humankind, until the late 1980s, action was not a major target of research in the behavioral, cognitive, and brain sciences. However, over the past two decades, the situation has changed considerably. Interest in action and its relationship with cognitive functions like perception, attention, memory, and volition has surfaced in parallel in a number of independent approaches at both the experimental and the theoretical level.

Unlike other recent treatments of the emerging field of action science, this book neither examines the field from one coherent perspective (cf. Pecher & Zwaan, 2005; Rosenbaum, 2010; Schmidt & Lee, 2010) nor tries to provide an all-embracing survey of the recent surge of action research (cf. Morsella, Bargh & Gollwitzer, 2009). Instead *Action Science: Foundations of an Emerging Discipline* deliberately presents the field in terms of

its diverse major theoretical and methodological approaches and thus provides a forum for comparing them with each other. Each of these approaches is portrayed as a tutorial by leading proponents of the perspective in question.

However, before exploring the emergence and current landscape of action science in terms of constitutive leitmotifs and approaches in further detail, let us briefly address a more fundamental question, namely, what actions actually are.

Actions

Action takes diverse forms; therefore the formulation of a working definition of action is no easy undertaking. First of all, we need to ask what kind of entity counts as an action. Given that our actions are embedded in a continuous stream of ongoing behavior, we need to fix criteria to parse this stream. What kind of information can be used for determining the beginning and end of an action?

Sometimes the answer to this question seems obvious. Turning off the alarm clock starts with the perception of the ringing bell and ends with the pressing of a button to stop the intrusive sound. This action closely resembles the pressing of a key in a reaction time experiment. However, actions are not always that simple and short-lived. When it comes to more complex and longer-lasting endeavors like getting dressed, gardening, or leading a discussion, action individuation might be less obvious. On the one hand, we have no such salient perceptual event as a ringing bell indicating the onset of the action. Given that, for instance, reaching for one's trousers might be embedded in other activities like yawning and stretching, transitions between different actions are sometimes extremely difficult to detect. On the other hand, extended actions always consist of a number of segments, each of which could also be considered as a discrete action. To dress, one has to search, grip, and put on different garments in turn. This increases the chance of interruptions and discontinuities in the unfolding action, leading to a loss of perceptual coherence. Thus the more complex the action becomes, the less reliable perceptual events are for action individuation. Research on action often tries to avoid this problem by focusing on well-individuated and short-lived actions in tightly controlled experimental settings. However, when we talk about everyday actions, one must keep in mind that we often have no obvious and unambiguous way of parsing the continuous stream of ongoing behavior (Stränger & Hommel, 1996). If perceptual events do not suffice, then how do we determine the beginning and end of an action?

Most of the current approaches in action science address this problem by individuating actions in terms of their underlying goals (see chaps. 2–5, 8–11, 13–16). Accordingly, an action starts with the first behavioral activity directed toward a particular goal and terminates with the achievement of the goal (Maasen, Prinz & Roth, 2003). This notion implies that an action goes beyond a simple body movement. Instead it is composed of two elements: the first is ongoing behavioral *activity* (i.e., body movements); the second is the orientation of these movements toward a prospective *goal* state (i.e., toward the effect created by these movements).

This first working definition of action thus comes along with the issue of understanding what goals actually are. However, when it comes to goals, things can become precarious. This is because the term "goal" is used both as a descriptive and as an explanatory term, in various different ways. At a *descriptive* level, we use the term "goal" to characterize, in an economical way, the behavior of systems whose actions are apparently directed toward the achievement of certain goals-in-the-world. In this respect, the behavior of humans, animals, plants, and even air conditioners can be considered to be goal directed. For instance, an endurance runner behaves in a certain way to reach the finish line, a pigeon behaves in another way to return to its dovecote, and an air conditioner behaves in yet another way to control the temperature. Accordingly, all these different systems show a variation of means to bring about an end (see chap. 6). However, the term "goal" is not exclusively used to describe the behavior of systems in the outside world (i.e., from the third-person perspective). In fact, with respect to our own actions, we often use the same term to describe our own explicit mental representations of the goal states to which our actions are directed. Such goals-in-the-mind described from a first-person perspective are often charged with an intentional meaning. According to the testimony of introspection, we do not simply cross the street to reach the other side but do so because we *want* to. In fact, the feeling of intention is so powerful that we even tend to reconstruct the behavior of artificial objects as driven by goals-in-the-mind (Heider & Simmel, 1944).

However, using the term "goal" in a descriptive way to characterize action does not tell us anything about whether goals actually play a functional role in action. Concerning goals at an *explanatory* level, there are two classical answers to this question. One answer roots goal-directed behavior in procedural routines that have evolved through phylogenetic (Tinbergen, 1951) or ontogenetic learning (Thorndike, 1911). Importantly, it is assumed that these procedural routines do their work without the active involvement of goals. For instance, Tinbergen's sticklebacks show

complex display and spawning behavior because these stimulus-triggered reactions have turned out to be successful in the course of evolution. Likewise, Thorndike's cats escape the puzzle box because they have learned, through trial and error, that solving the puzzle box is followed by a reward. Thus the exemplified behavior of sticklebacks and cats is assumed to be *directed at* but not *driven by* goals (i.e., the term "goal" is used only in a descriptive but not in an explanatory manner). In contrast, the second answer roots goal-directed behavior in the activity of goal representations (i.e., goals-in-the-mind) arising from motivational processes. This idea is not only deeply embedded in our commonsense psychology but also part of scientific theories of motivation and volition (e.g., Ach, 1910; Bargh, 1996; Gollwitzer, 1996; Heckhausen, 1991; Miller, Galanter & Pribram, 1960) that consider internal representations of goal states as an essential part of the intention to act. The term "intention" is thus often used as a blanket term for all kinds of internal representational structures linking suitable actions to action goals. However, in this view, goals have, in a way, two faces: actions are driven by and directed at goals; thus goals are used both for describing and for explaining action. It appears that such a dual usage carries the risk of mixing up both levels, thus treating descriptions as explanations and vice versa. In fact, we can easily assign declarative goal representations to each and every action at will. Nevertheless, saying that, for instance, "opening the door" is driven by the goal representation of "opening the door" is, as a start, nothing but a tautological extension of describing actions.

To avoid circularity, the explanation of actions in terms of goals thus has to go beyond introspective experience. One possibility is to categorize goals with respect to the requirements placed on action planning and execution (Prinz, 2008). Such a categorization has to consider different types of goals. First, goals might differ in that they are located *within* or *beyond* the current range of objects or things to which the actor has perceptual access. Goals within the perceptual range, like grasping a glass of water, can be specified in terms of spatial coordinates. Such goals are typically investigated in research on motor control and attention (see chaps. 2–4 and 9) using, for instance, aiming movements of the hands (cf. Jeannerod, 1988; Rosenbaum, 1980) or eyes (cf. Deubel & Schneider, 1996; Kowler, 1990). In this context, goals are often referred to as targets. Importantly, target representations can be based on the current perceptual input in most instances. In contrast, realizing goals beyond the actor's current perceptual range typically necessitates a situational change. For example, dressing first requires opening the wardrobe door to see, take out, and

finally put on one's favorite shirt. Accordingly, goal representations involved in these kinds of actions have to be based on anticipations of future states that are not yet specified in the current perceptual environment (see chaps. 5, 13, and 16; but see chaps. 6 and 7). Second, *abstract* and *concrete* goals place different requirements on action planning and execution as well. The realization of abstract goals, like "taking a trip around the world," often covers a protracted time range when compared to concrete goals, like "switching on the light." Therefore abstract goals are more loosely connected to specific actions than are concrete goals (see chaps. 5 and 16). A related third differentiation that we will come back to later on concerns *cold* and *hot* goals, which differ with respect to their propositional attitude. For instance, the goal of "attending a conference" is certainly not as pressing as the goal of "quenching one's thirst." Hot goals require an active process of searching for the right opportunity for action execution, whereas cold goals might simply wait for the right opportunity to arise.

Naturally, this systematization is meant to be neither exhaustive nor unrivaled. Each of the current approaches in action science has, in fact, taken its own position when dealing with the elusive term "goal." Yet whatever the prime explanation of action is, current approaches agree on the notion that every action builds on two kinds of antecedents: first, the *external* world providing and suggesting action opportunities; second, the *internal* state of the actor that needs to interact with external opportunities. Accordingly, actions are not mere reflexes solely determined by the external environment. Likewise it certainly does not suffice to consider actions as simple incarnations of internal factors detached from the current situation. To conclude, as a first approximation and working definition, actions can be considered as body movements that depend on external and internal factors and are directed toward a prospective goal state.

Action Science

Actions are studied in many fields of research, including motor control, experimental and cognitive psychology, cognitive neuroscience, philosophy, sports science, and developmental psychology. A prominent research question is identifying *what* people or animals do given specific external and internal circumstances and *why* they do it. This kind of research may be termed *What-research* and is mainly interested in the antecedent conditions for action. Concerning the internal state of the actor, relevant questions address, for instance, where goals or intentions come from (issues of motivation) and what energizes their pursuit and shelters them from

competing distractions (issues of volition) (Gollwitzer, 1999). Another major concern of research is to understand *how* people actually realize a given goal in the current situation by acting. This kind of research is mainly interested in the functional architecture of the underlying mechanisms giving rise to action. This may be termed *How-research*.

We realize, however, that the dividing line is not really sharp. Thus, separating What- and How-research does not deny mutual dependence between the generation and realization of goals. In fact, past experience of how to achieve an effect provides options for what one may intend to do now (see chap. 5). Conversely, what one intends to do now provides options for action evaluation and refinement and thus affects the way one will act in the future (Herwig, Prinz & Waszak, 2007; see also chaps. 2, 3, 4, and 16, this volume). Nevertheless most current approaches in action science emphasize How-questions over What-questions and leave issues of motivation and volition to participants' willingness to follow the experimenter's instructions. Furthermore, within the broad field of full-fledged actions in everyday life, most approaches concentrate on the study of the functional underpinnings of short-lived and well-individuated actions for methodological reasons. This state of affairs is also mirrored by the contributions in this book.

With these preliminaries in mind, we now turn to briefly look at the history of action science. This may help to understand why it took such a long time for action to become a major target of research in the behavioral, cognitive, and brain sciences. It can also help to appreciate that current issues in action science are far from being settled. Instead action science seems to have just entered adolescence and a thrilling phase of its development.

Action Neglect

There is a long-standing tradition to simplify the complexity of the mind and the brain by viewing it as an "input–output system" in which perception goes in and action eventually comes out. It has often been pointed out that research on the input side has long dominated research on the output side in the behavioral, cognitive, and brain sciences (e.g., Jeannerod, 1985; Gazzaniga, Ivry & Mangun, 2009; Rosenbaum, 2005; Schmidt & Lee, 2010). The reasons for this imbalance are manifold, some reflecting the scientific Zeitgeist and others pointing to more fundamental problems in both methodology and theory.

Historically, the scientific study of the mind and brain has emerged from epistemological questions concerning the nature, acquisition, and scope

of knowledge. Epistemological questions about how a world is made inside of organisms focused, by their very nature, more on the input than on the output side. However, at the end of the nineteenth century, when psychology developed as an independent scientific discipline, researchers made promising attempts to complement research on epistemology and perception with research on processes underlying volition and action. Most notably, at that time, Lotze (1852) and James (1890/1981) fathered the ideomotor principle, which was one of the first theoretical approaches to address the cognitive underpinnings of voluntary actions. According to ideomotor theory, ideas or mental images (i.e., representations) of events that reliably followed our movements in the past gain the power to evoke the corresponding actual movement. Besides this early elegant piece of armchair psychology, Ach (1905) was the first to address volition and action experimentally by investigating the intricate interplay between representations of intended effects (*Zielvorstellungen*) and representations of the current environment (*Bezugsvorstellungen*). This research culminated in his theory of determining tendencies (Ach, 1910). However, unfortunately, these early attempts to establish research on the output side did not continue and soon fell into oblivion during the first part of the twentieth century, when other approaches started to dominate psychology.

In Europe, the evolving Gestalt psychology tied in with its epistemological roots and thus mainly focused on perceptual issues. The few exceptions (Lewin, 1926; Gottschaldt, 1954) that have also taken action into account were descriptive rather than explanatory in nature. At roughly the same time, behaviorism started to dominate psychology on the other side of the Atlantic. Highlighting the output side as the only permitted source of psychological data, this approach paved the way for analysis of muscle activity and body movements. However, behaviorist thinking ousted discussions about internal events in the "black box" as well and reduced actions to simple, observable behaviors solely depending on and reinforced by external stimuli (for an exception, see Tolman, 1932). Thus behaviorism left no room to investigate the intricate interplay between external and internal factors in the control of action.

The analysis of internal mental representations became popular again when cognitivism started to reject behaviorism in the 1960s, but now psychology passed up the chance to inherit behaviorism's interest in the output side. Instead cognitive sciences focused again on the input side, namely, on the study of "stimulus information and its vicissitudes" (Neisser, 1967). In fact, cognitivism not only preferred just the analysis of cognitive functions related to the input side but also disfavored the study of the

output side. According to the baby-with-the-bathwater hypothesis (Rosenbaum, 2005), actions were disfavored because they were spuriously associated and equated with a mindless response-centered program of behavioristic research. Ironically, with regard to methodology, cognitivism was, however, not able to completely abandon actions. In fact, to gain insight into cognitive functions related to the input side, cognitive research relied heavily on reaction time methods. These methods work only as long as subjects execute certain agreed-on actions (output) as soon as they reach certain cognitive states (input). However, in this context, reactions serve only as a test probe and not as an object of investigation.

More generally, the methodology of experimental research promotes the imbalance between research on the input and research on the output side. In experimental settings, the researcher typically manipulates external stimulus conditions and measures the effects of these manipulations on the participant's mental life and behavior. In the context of perception, a tight causal relationship seems to exist between the external conditions provided by the experimenter and the sensations and perceptions of the participant. What the subject perceives depends largely on the given stimulus condition. In the context of action, however, this causal relationship seems to be more fragile. What the subject actually does depends only partly on the given stimulus condition. Accordingly, experimental research in the context of action has to manipulate (or at least control via instructions) internal conditions like intentions as well, which are by their very nature less accessible. Moreover, action research often has to face the methodological problem that the participant's room for maneuver is restricted by the methods of measurement. This problem is of particular relevance in research on the neurophysiology of action. For instance, early neural recording techniques necessitated the use of an anesthetized animal and thus precluded action research but not research on sensory processes (Evarts, 1973). Although these early problems were later overcome by technical progress, even the accuracy of modern technologies used for recording brain activity (e.g., electroencephalography, functional magnetic resonance imaging) is severely impaired by excessive body movements.

It is evident that problems in methodology go along with related problems in theory. To control internal factors, we must address tough theoretical questions: What internal factors should we focus on? In what way are these factors represented? How do they interact with external factors? How do they contribute to the control of action? Although these questions arose very early (e.g., Ach, 1905; James, 1890/1981; Lotze, 1852), psychology and neurobiology deferred providing conclusive answers for a long time.

However, over the past decades, signs are mounting that the neglected status of action is about to become history.

Action Turn

Renewed interest in action has surfaced in a number of independent approaches and fields of inquiry in the behavioral and brain sciences. One fundamental contribution came from research on motor control and learning, which started to flourish when the fields of motor behavior and neurophysiology began to share common problems and methods in the early 1970s (Schmidt & Lee, 2010). The following years witnessed a great deal of research concerned with how the central nervous system coordinates the many individual muscles and joints and how sensory information from the environment and body is used in the control of body movements and stabilization (e.g., Franklin & Wolpert, 2011; Wolpert & Kawato, 1998). Moreover, research increasingly addressed the question of how movements are learned, that is, how movement production changes as a result of practice and experience (e.g., Adams, 1971; Schmidt, 1975). Influenced by the cognitive revolution, the field simultaneously changed from having a task-oriented perspective to a more process-oriented view on movement. Focusing on the mental and neural events underlying movement control and learning, this transition paved the way for the connection of the long-standing tradition of research on motor functions with research in cognitive domains (Rosenbaum, 2010; see also chaps. 2, 3, and 4, this volume).

Another line of renewed interest in action came from the revival of ideomotor theory in the 1970s and 1980s (Greenwald, 1970; Prinz, 1987). By emphasizing strong links between action representation and execution, this approach offered an answer to the question of how goal-directed actions are possible at all. As mentioned earlier, the basic ideas of ideomotor theory were already spelled out in the nineteenth century (Lotze, 1852; James, 1890/1981) but fell into oblivion during behaviorism and the early days of cognitive sciences (see Stock & Stock, 2004, for a historical overview). According to ideomotor theory, actions are represented by their sensory effects on the body and environment and can thus be triggered by activating these effect representations either endogenously (e.g., *thinking* of the effect) or exogenously (e.g., *perceiving* the effect) as long as conflicting effect representations are absent. Importantly, links between actual movements and the sensory effects of the movements are assumed to arise from learning. Acquiring associations between movements and their perceivable effects can thus become functional in two ways. First, associations allow prediction of the outcome of given movements (forward computation).

Second, they allow selection of appropriate movements to achieve an outcome given anticipatory effect representations (backward computation). Accordingly, goal-directed actions are possible through backward computation if anticipated effect representations are congruent with the goals of the agent (chap. 5).

Renewed interest in action also emerged in the field of research on attention. In the 1980s, researchers began to question the traditional idea that attentional selection is due to limited processing resources. Instead they proposed that selection arises because humans, given their limited number of effectors, are constrained in the number of actions that they are able to perform at one time (Allport, 1987; Neumann, 1987; Van der Heijden, 1992). Consequently attention began to be viewed as a prerequisite to determine what objects should gain access to the limited effectors and which object-based action should be initiated. These ideas established the basis for investigating the interplay of attention and action in further detail (cf. Deubel & Schneider, 1996; Humphreys & Riddoch, 2005; Schneider, 1995; chap. 9, this volume).

A further boost for research on action emerged from neurophysiology and neuropsychology. Single-cell studies led to the discovery of a specific class of neurons (mirror neurons) in the monkey's premotor cortex, emphasizing a strong link between action production and perception. These neurons fire both when animals perform actions and when they observe similar actions performed by other individuals (Gallese, Fadiga, Fogassi & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese & Fogassi, 1996). Subsequently, mirror neurons have also been found in the human brain, coding the goals of actions rather than the movements that are made (Rizzolatti, Fogassi & Gallese, 2001; chap. 8, this volume). Interest in action was also fueled by a single case study of a woman, D.F., who suffered damage to the ventral pathway of her visual system (Milner & Goodale, 1995). Although D.F. was not able to recognize and report the orientation of a presented slot, she had no problems with inserting a card into the slot with her hand. On the basis of this observation and previous research, Milner and Goodale suggested that there are at least two visual systems: A "how" visual system for action and a "what" visual system for object identification. Consequently, research on visual perception became increasingly interested in research on action (for recent reviews and extensions, see Gangopadhyay, Madary & Spicer, 2010; Kravitz, Saleem, Baker & Mishkin, 2011).

Increasing interest in action was also observable in developmental and social psychology. On the one hand, progress in video-recording techniques led to an increased use of actions as a means of investigating the development

of cognitive abilities in the preverbal child. On the other hand, reexamining Piaget's assumption that all knowledge is rooted in action, research on the development of action capabilities became a tradition in its own right (see chaps. 10 and 11). Moreover, research on neonates' ability to imitate facial gestures (Meltzoff & Moore, 1977) revitalized discussions about the possibility of an innately shared code for perception and action (Meltzoff & Prinz, 2002). Today research on imitation is a burgeoning interdisciplinary area helping to understand the mechanisms linking action perception and production (Hurley & Chater, 2005a, 2005b). In social psychology, a similar trend toward action emerged. For instance, research on people's tendency to mimic the actions of their interaction partners emphasized the importance of actions for modifying relationships between individuals (Chartrand & Bargh, 1999; see also chap. 13, this volume).

Another important contribution came from the emergence of ecological approaches and dynamical systems theory considering perception and action as intimately related. These approaches introduced important novel perspectives and techniques to the study of perception and action. For instance, ecological approaches stress the role of the perceiver's body and its action capabilities as a reference for detecting and using information for the formation of coordinated movement patterns (see chap. 7). Moreover, in contrast to cognitive approaches to action, ecological approaches adopt a strictly nonrepresentational stance. They rely on the extraction of action-relevant information provided and contained by the environment rather than on computational operations generating action programs (Gibson, 1979). Researchers who advocate dynamical systems theory often subscribe to the ecological approach and focus on describing ongoing cycles of perceiving and acting by using sophisticated quantitative techniques like differential equations (e.g., Kelso, 1995; Turvey, 1990; Warren, 2006; chap. 6, this volume).

Finally, an important new interest in action came from the emergence of the grounded or embodied cognition approach, which claims that high-level cognition, like linguistic and conceptual representations, is grounded in sensorimotor functions (Barsalou, 1999; Glenberg, 1997; Pulvermüller, 2005; see also chap. 15, this volume). Accordingly, embodied approaches offer an answer to the symbol grounding problem (i.e., how symbols get their meanings; see Harnad, 1990) inherent in classical cognitive approaches that view cognition as a modular system operating with amodal and arbitrary symbols.

Given these numerous independent lines for a revival of interest in action, it is perhaps not surprising that action control and learning have

recently emerged as a new topic for researchers studying artificial intelligence, especially in the domain of humanoid robotics (e.g., Kawato, 2008; Pfeifer, 2007; Schaal, 1999). Given the unsurpassed flexibility of actions that humans perform every day, we believe that—at least to date—research on nature's implementation of action control and learning is doing more to inform action implementation on machines than the other way around. However, we agree that this may change in the not-too-distant future, and one of our hopes for this volume is that the different approaches presented here will inspire more work on action in the artificial intelligence community.

As should have become clear in this brief sketch of the action turn in the behavioral and brain sciences, the current landscape of action science is split into a number of diverse approaches that exist more or less independently of each other. That is, action science as an emerging field of inquiry may suffer from the diversity of its constitutive approaches as long as different approaches coexist in parallel without coming into contact with each other. A prerequisite for resolving this issue is a resource that gathers all major approaches of action science and describes their latest state of the art. This book is meant to be such a resource. It is meant to provide a basis for comparing the different approaches with each other. Moreover, it is our hope that this book will help to start integrating the diverse approaches into a more coherent framework. As a preliminary step toward integration, the following section looks at action science in terms of theoretical leitmotifs that provide promising sources for finding similarities as well as contrasts in the diverse approaches.

Leitmotifs

Some major theoretical issues have, in more or less explicit ways, accompanied scientific debate on action ever since. As these issues have been with us in the past, they are likely to stay with us in the future as well, keeping action science busy over the coming decades.

Here we briefly touch on three leitmotifs of action research, trying to capture some of the gist of the debates associated with them. The first concerns relationships between perception and action, addressing ways in which the input and the output side of behavioral and cognitive activity may be linked to each other (in/out). The second concerns relationships between volition and action, addressing linkages and transitions between "cool" representational functions like perception and prediction and "hot" executional functions like intention and production (cool/hot). While

these two issues concern relationships between action and its major functional neighbors, the third pertains to levels of action explanation, that is, to the relative roles of high-level (cognitive) and low-level (sensorimotor) explanation and their mutual relationships (high/low).

In/Out

How are perception and action related to each other? While we do not have a comprehensive and coherent theory to answer this question, we do have an implicit working model: a framework that is implicitly shared by a number of otherwise diverse approaches. This model believes that relationships between perception and action rely on linkages (associations, connections, bindings, etc.) between tokens of perception and tokens of action. These linkages are thought to be acquired through learning (see, e.g., chaps. 2, 3, and 10). For instance, in a reaction time experiment, participants learn to link certain responses to certain stimuli, and they do so according to the mapping rules provided by experimental instructions. Notably, the linkages instantiated through these mappings are in most cases entirely arbitrary (e.g., pressing the left versus right key in response to red versus blue stimuli, etc.). In this regard, the logic of the experimental task can be seen to capture basic functional demands, to which organisms are exposed in natural settings. To be in a position to act and react in a meaningful and successful manner, they need to create, through continuity-based operations of instrumental learning, a gigantic machinery for appropriate mapping of action to perception (see chap. 12).

These mappings must be arbitrary because they link incommensurate entities. Stimuli on the perceptual side differ from each other in terms of sensory features like, for example, color, shape, and size. Conversely, responses on the action side differ in terms of motor features like direction, amplitude, force, and others. Accordingly, stimulus features have no way to specify or determine response features by themselves. The sole way of linking them to each other is through creating arbitrary mappings. Once established, these mappings mediate between perception and action as a dictionary mediates between two incommensurate vocabularies: they provide the ground for translating, as it were, the vocabulary of perception into the vocabulary of action (Massaro, 1975, 1990; Welford, 1960, 1968, 1980).

So far so trivial, perhaps. By and large, the implicit framework captured by the translation metaphor has been fairly successful. While different approaches to action have couched it in different theoretical languages, it seems to have no strong competitor, perhaps suggesting that the translation

metaphor may simply be valid and true. Yet even if we accept it as true by default, we still have reasons to doubt that it gives us the full truth. A substantial body of evidence challenges the classical translation framework, arguing for a role of similarity-based *matching* on top of contiguity-based *mapping*.

Much of this evidence comes from the domain of action representation, more specifically, from studies demonstrating relationships between perception of (foreign) action and production of (own) action that appear to be based on action content. Such mappings often appear to be similarity based, such as in imitation (Meltzoff & Moore, 1977; Piaget, 1962; Prinz, 2002), social mimicry (Chartrand & Bargh, 1999; Chartrand & Dalton, 2009), or ideomotor movements (Knuf, Aschersleben & Prinz, 2001; Prinz, 1987), suggesting operations of nonarbitrary, similarity-based induction of action through perception rather than arbitrary, contiguity-based translation between perception and action (matching, not just mapping).

To account for such content-based relationships, it has been suggested that human minds/brains may, on top of their general-purpose machinery for contiguity-based mappings, also have more specialized modules for similarity-based matching at their disposal. To allow similarity-based induction, these modules must rely on shared representational resources for perception and action—a shared representational space for the perception of foreign action and the production of one's own action. Input- and output-related entries in this representational space are therefore entirely commensurate. As they share common representational dimensions, they may now induce each other by virtue of representational overlap, or similarity (Kornblum, Hasbroucq & Osman, 1990; Kornblum, 1992). These are the basic claims that the principle of common coding invokes for the mind (Prinz, 1990; Prinz, 1997) and the mirror neuron system instantiates in the brain (Rizzolatti & Sinigaglia, 2008; Pineda, 2009; chap. 8, this volume).

Since imitation is often a spontaneous and seemingly automatic consequence of action perception (see chap. 12), it may be tempting to consider similarity-based induction a simpler and more direct mode of linkage between perception and action as compared to contiguity-based translation. However, we need to be careful not to confuse apparent automaticity with functional simplicity and directness (as one should always deeply distrust the claim that something in the mind/brain is direct and simple). In fact, while it may be true that matching through induction (based on representational overlap) is by itself a less complex operation than mapping through translation (based on arbitrary linkages), we must not forget that

the creation of a common representational space requires additional translation work.

Such work is required for translating entries from the sensory and the motor domain (which are incommensurate with each other) into a common representational domain where they become commensurate. There are three basic ways of solving this problem (Prinz, 1984): (i) translating sensory entries into a motor language, (ii) translating motor entries into a sensory language, and (iii) translating both into a third neutral language. The first option is chosen by motor theories of speech and action perception (Lieberman, Cooper, Shankweiler & Studdert-Kennedy, 1967; Weimer, 1977; Galantucci, Fowler & Turvey, 2006; see chap. 8, this volume). These theories claim that perceptual representations of incoming stimuli (e.g., auditory or visual) are mapped onto motor representations of actions required to produce them, to the effect that matching through induction becomes possible in the motor domain. The second option is chosen by ideomotor theories of action production (James, 1890/1981; Prinz, 1997; Hommel, Müsseler, Aschersleben & Prinz, 2001; see chap. 5, this volume). They claim that motor representations of outgoing responses are mapped onto perceptual representations of sensory features of their outcomes, to the effect that matching through induction becomes possible in the sensory domain. The third option is chosen by cognitive approaches to action control, claiming that sensory stimuli and motor responses are both mapped, or translated, into a common cognitive domain—for instance, a domain for semantic representation of meaningful events (see chaps. 4 and 11).

Accordingly, there is a price to be paid for the enabling of matching-through-induction on top of mapping-through-translation. The price is paid by additional translation work that is required to make similarity work and induction possible. Mirror neurons in premotor areas, for instance, can do their job of matching perception to action only by virtue of entertaining smart and highly specialized mapping relationships with neurons in both the sensory areas taking care of perception and the motor areas taking care of production.

This raises the question of what similarity-based matching can do for us beyond contiguity-based mapping. Why should nature invest scarce resources for building a module for matching on top of already existing machinery for mapping? While we have no way of knowing the true answer to such a question, we may still speculate. That the module seems to be dedicated to taking care of relating production of one's own action to perception of foreign action invites the speculation that its proper function may pertain to social interaction rather than individual action. Similarity-based

matching between one's own and foreign action may be seen to enable spontaneous social resonance and alignment (see also chap. 13). For social animals like us, investment along these lines may well pay off.

Cool/Hot

However close and intimate relationships between perception and action may be, it would certainly be misleading to consider action an automatic consequence of foregoing perception. As explained at the beginning, action, by definition, builds on two kinds of antecedent conditions, external and internal. While external circumstances are represented through perceptual functions, internal circumstances are represented through intentional functions. Broadly speaking, intentional functions stand for the driving forces that make things happen. While perception is required to select an appropriate action, intention is required to initiate and realize it.

As stated earlier, the contributions to this volume focus very much on "cool" approaches to action, emphasizing the role of perception and cognition at the expense of "hot" intention and volition. On the one hand, such selective focus is always justified in science—perhaps even a prerequisite to successful scientific inquiry. On the other hand, we need to take care not to be overselective and disregard the functional role of intentions and their dynamics altogether. The problem with a selective approach like this is that it may lead us to see intentional functions and operations as reflecting somewhat mysterious forces, arising from the dark and unexplored realms of drives, needs, and desires. An example of such a mysterious force is provided by William James's famous discussion of the workings of the will. James had no more than an enigmatic Latin word to connect the cool and the hot: "Fiat!" was the term with which he denoted the hot voluntary impulse that makes an action happen when cool cognitive conditions are fulfilled (James, 1890/1981, Vol. 2, p. 501).

The reasons for the relative neglect of the hot sources of action appear to be rooted in both method and theory. Regarding method, it is fairly obvious that hot internal contributions to action are less easy to access and assess than cool internal contributions. While perception is linked to external events that can be experimentally controlled, internal contributions are by their very nature less controllable from the outside. A similar difference applies to theory. While perceptual representations and functions refer to states of affairs that are given in the current environment, intentional representations and functions refer, by definition, to states of affairs that are currently not given (planned to be realized through appropriate action instead). With respect to both method and theory, intentional

contributions to action are therefore much more elusive than perceptual contributions. Accordingly, we should not be surprised to find them somewhat neglected.

Still, we have reason to believe that the future of action science will very much depend on finding ways of convincingly integrating the cool and the hot. More specifically, action science needs to develop theoretical approaches that relieve the hot drivers of action from their enigmatic flavor and allow the combination of the operation of external/perceptual and internal/intentional factors within a single and coherent framework.

While some of the approaches presented in this book already address such integration explicitly (see chaps. 14 and 16), others offer themselves as pertinent extensions. As an example, we may consider the ideomotor approach to voluntary action discussed in Hommel's chapter 5. This approach can easily be extended to combine the operation of cool and hot factors in a single, coherent framework. Here one may even claim that the extension is not really an extension because it does not require the introduction of novel theoretical principles but rather an elaborate explication of basic claims that are already inherent in the approach.

As Hommel outlines, ideomotor theory posits two basic principles, one for learning and another for control. Ideomotor learning claims that (representations of) actions become associated with (representations of) action effects or outcomes they lead to. Such action effects span immediate sensory consequences of ongoing movements (like pushing a doorbell button) and remote environmental events that follow from these movements (like the ringing of a doorbell). Likewise, ideomotor control claims that, once acquired, these associations can also be used in the reverse direction, linking representations of action outcomes with representations of actions leading to them. These reverse links offer an explanation for goal-directed, voluntary action. The ideomotor theory of voluntary action claims that representations of intended action effects (i.e., goals) have the power to elicit actions that are suited to realize them (i.e., of which previous ideomotor learning has shown that they may lead to these effects). This is, in a nutshell, what William James's ideomotor principle claims. It invokes transition from mere representation to real execution as expressed in the enigmatic Latin word.

While the ideomotor framework addresses the mechanics of learning and control, it fails to address the dynamics of volition. For example, it takes representations of intended action outcomes for granted without explaining (1) when and how such intentional representations are formed and (2) in what way they differ from nonintentional kinds of action representations

(that do not possess the power to realize the actions they refer to, e.g., percepts, thoughts, and anticipations).

To account for these remarkable properties, we need to complement the mechanics of learning and control with the dynamics of motivation and volition. Without going into any detail, we may envisage two obvious extensions, one pertaining to learning and another pertaining to control. In regard to learning, the extension claims that action outcome learning includes a dynamic component of outcome evaluation—an automatic assessment of action outcomes in terms of the actor's current needs and desires. With this extension, action outcomes turn from neutral to more or less desirable or undesirable events. Accordingly, we may think of outcome representations as being characterized in terms of both cool links to instrumental actions leading to them and hot links to dynamic evaluations pertaining to them. Conversely, regarding control, we may envisage a sequence of events in the reverse order. Here we may conceive of intention formation as a process that starts from given dynamic states (i.e., needs and desires) and then determines action goals that are desirable or undesirable in terms of these states.

According to this view, the crucial functional feature that distinguishes intentions from other kinds of action-related representations (like percepts, thoughts, or anticipations) derives from their origin in dynamic states. Intentions are, from the outset, charged and energized by motivational drivers like needs and desires. It is these drivers that make the difference. They furnish intentions with the power to make things happen by moving from representation and prediction to execution and production.

This is, of course, no more than a brief sketch of ideas for a dynamic extension to the mechanics of ideomotor theory. One of its important implications is that it construes close functional links between perception and volition. According to the extended framework, perceptual and intentional underpinnings of action are both acquired in the same learning processes, and likewise they are both combined in the formation of intentions for control. As a result, the dynamics of volition use the same kinds of representational resources as the mechanics of perception and cognition. While intentions and action goals originate from dynamic sources, they are created and maintained in the same representational domain that takes care of the mechanics of action and event representations. Action, event, and goal representations are all made of the same stuff: they stand for events that happen, have happened, may happen, or ought to happen.

While this example applies to the ideomotor approach, other approaches may require different kinds of extensions. The claim here is not that cap-

turing the hot side of action requires one to subscribe to ideomotor theory but that the future of action science requires us to take serious steps to integrate cool and hot contributions into coherent theoretical frameworks for action. Ideomotor theory is just an example, showing what such steps may look like.

Low/High

Scientific debates address both questions and answers. In fairly advanced fields, they will typically address competing answers to questions on which the field has settled, that is, competing explanatory programs for the things to be explained. In less advanced fields like action science, however, they will often address the issue of which kinds of things should be studied and what research should be asked, in other words, what research programs should be followed in the first place. One such debate in action science—actually a never-ending one—concerns the proper way and the proper level of action description and explanation.

This issue is far from trivial. As said earlier, when we talk about actions, we talk about units of activity that we as observers segment and individuate from a continuous stream of ongoing activity. What counts as an action is therefore determined by science, not by nature. Accordingly, we need to justify how we segment this stream and how we individuate units of activity. How should we describe action? What counts as a meaningful unit of analysis? What kinds of criteria do we use for segmentation and individuation? Should we, for instance, consider muscle contractions or limb movements? Should we consider brief interactions with external objects and events like grasping a cup or catching a ball? Or should we even consider long-term endeavors like, for example, traveling around the world? Depending on our choice on this scale, we may come up with entirely different sets of research questions and entirely diverging research programs.

How can action science deal with such diversity? There are orthodox and liberal views regarding the importance of competing levels of analysis. Orthodox views tend to single out one particular level without giving much credit to other ones. Such views are often justified by the claim that the level chosen is the true and proper one for understanding action. More liberal views tend to consider two or more levels simultaneously and explicitly address the issue of how operations at different levels may relate to each other. How can low-level sensorimotor operations instantiate high-level cognitive actions and interactions? Conversely, how can cognitive plans and intentions recruit appropriate sensorimotor operations? We

believe that questions like these lie at the heart of present and future action science. If action science is to become more than an assembly of coexisting approaches and research programs at different levels of analysis, we need to find ways to relate low-level micro-operations to high-level macro-procedures.

As a first step to achieving this, we need to take issue with orthodoxy. To simplify matters, we may consider two levels of analysis, low and high (sensorimotor and cognitive). Sensorimotor orthodoxy claims that actions are basically made up of sensorimotor operations. As a consequence, this view regards low-level operations as the proper level of description and explanation. While it may acknowledge that action may be preceded and accompanied by high-level cognitive operations, it treats them as a cognitive cover story that bears no causal significance for action control. Conversely, cognitive orthodoxy claims that actions are basically generated and controlled through operations at the cognitive level so that the language of cognitive mechanisms provides the proper level of description and explanation. While it may acknowledge that these high-level operations need to be instantiated through the workings of low-level sensorimotor machinery, it treats this machinery as a trivial slave system that bears no causal significance for control.

Accordingly, both kinds of orthodoxy resort to the same strategy for defending their deliberate ignorance of concurrent operations at other levels of processing: while they admit their existence, they deny their functional relevance. It is difficult, however, to see how such denial can be justified. While reasons may exist to posit that operations at one level constrain operations at other levels, it is hard to see why the intrinsic machinery of the constrained level should play no functional role at all. As always in science, we need to face the possibility that operations that are constrained by operations at other levels may still lead their own functional life, thus and thereby contributing to the pattern of resulting action. This argument is already closely related to the basic tenets on which more liberal views of relationships between processing levels converge. Liberal approaches may take two basic directions, proceeding either from high to low or from low to high. The two directions differ with respect to both method and theory. High-to-low approaches will typically study high-level "cognitive" tasks, aiming at demonstrating the latent workings of sensorimotor operations in cognition. Accordingly, their theoretical language speaks of *embodied cognition* and of high-level semantics *grounded in* low-level sensorimotor operations (see chap. 15). Conversely, low-to-high approaches typically study sensorimotor tasks, aiming at demonstrating

the latent workings of cognition in sensorimotor performance. Their theoretical language speaks of *cognitive control* of task performance, and low-level sensorimotor processing *constrained by* high-level representations and operations (see chap. 4).

It should not go unnoticed that the divide between the "high" semantics of cognition and the "low" kinematics of movements is, at the same time, a divide between declarative and procedural processing resources. The claim that operations at high and low levels may interact with each other thus poses a challenge to the functional divide that often seems to exist between declarative *knowledge about action* and procedural *knowledge for action* (at high and low levels, respectively). One such challenge comes from high-to-low approaches. For these approaches, the explanandum resides at the level of declarative processing, whereas procedural processing takes the role of the explanans. The basic assumption here is that the gap between the two is bridged by semantic information being grounded in motor information. Meaning is grounded in movement: there can be no meaning without movement. The other challenge comes from low-to-high approaches. For these approaches, the explanandum resides at the level of procedural processing, whereas resources and operations at the declarative level take the role of the explanans. Here the basic assumption is that motor information is constrained by semantic information. It is thus claimed that movements are grounded in meaning: there can be no movement without meaning. Both approaches hold that the functional gap between declarative and procedural resources for action is continuously bridged by automatic and mandatory cross talk between them (Prinz, Diefenbach & Springer, in press).

Of course, we should consider the notion of continuous cross talk a first and still fairly preliminary answer to the underlying questions. As said earlier, we believe that the future of action science will very much depend on elaborating on this notion and developing more detailed views of structural and functional relationships between high and low levels of action processing.

Overview

To conclude, we briefly provide an overview of the following chapters. The contributions in this book are grouped into six parts differing with respect to either their theoretical and methodological background or their content domains (i.e., kinds of actions and associated cognitive processes under study). Part I addresses core issues of action science. These core issues focus

on questions about how actions are controlled and learned (Heuer & Sülzenbrück; Taylor & Ivry; Rosenbaum; Hommel). The following five parts cover important extensions of the field. Part II presents ecological approaches to action, focusing on questions about how organisms make their way in the world and how action modulates perception (Turvey; Proffitt & Linkenauger). Part III analyzes the neural underpinnings of action understanding and the close coupling of action and attention (Rizzolatti & Sinigaglia; Humphreys). Part IV concerns developmental perspectives on action science and focuses on the interplay of action and cognitive development, as well as action perception and production in infancy (von Hofsten; Meltzoff, Williamson & Marshall). Part V explores social perspectives of action science concerning the core mechanisms of imitation and joint action (Heyes; Loehr, Sebanz & Knoblich). Finally, part VI addresses high-level issues of action science and deals with action experience and the relationship between actions and the conceptual system, as well as between volition and action (Chambon & Haggard; Kiefer & Barsalou; Goschke). Here we provide a brief overview of the individual contributions in each of the six parts.

Part I: Control and Learning

Part I presents four approaches addressing the core questions of action control and learning. The first three approaches primarily emerged from motor research and thus pay more attention to specific movement characteristics than the fourth approach, which originates from ideomotor theorizing and is mainly interested in the final state of a movement. Accordingly, it is perhaps not surprising that the actions under study in the different chapters range in a descending order of complexity and contextualization from tool use actions requiring complex transformations to more or less simple keypress actions. However, despite these differences, the authors of the first four chapters agree that actions are controlled by mental representations—be it in the form of internal models or action-effect associations—that have been built up or refined in the course of previous experience.

The opening chapter, by Herbert Heuer and Sandra Sülzenbrück, is concerned with tool use actions. More specifically, the authors address how complex transformations between the actor's body movements and the resulting movements at the effective tip of a tool (e.g., a lever) are mastered and how an internal representation of such a tool transformation is acquired. Issues discussed include the accuracy of the internal representation, transparency and awareness of the transformation, the influence of

aging on learning the transformation, the impact of distality between the actor's body movements and the movement at the effective tip of the tool, and finally the incorporation of tools into the body schema.

In chapter 3, Jordan Taylor and Richard Ivry examine the role of awareness (i.e., of explicit and implicit processes) in the study of skill acquisition and refinement. Separating an action-planning phase mainly responsible for goal selection and an action execution phase mainly responsible for goal realization, the authors focus on two model tasks: the serial reaction time task and visuomotor adaptation, emphasizing action planning and execution, respectively. They propose that to optimize future actions, explicit processes related to action planning and implicit processes related to action execution use different error signals. Accordingly, explicit processes use performance errors, which help to define what the desired movement should be, whereas implicit processes use prediction errors between a desired and actual outcome to help refine the implementation of the desired movement.

In chapter 4, David Rosenbaum argues that planning and controlling one's physical actions are first and foremost a cognitive endeavor. This statement is discussed with reference to four problems of action control: perceptual-motor integration, sequencing and timing of actions, action selection among alternatives, and the learning of skilled action. For each of these problems, Rosenbaum presents the early ideas of major thinkers in combination with the illustration of current research speaking for the cognitive foundations of action planning and control.

Finally, in chapter 5, Bernhard Hommel presents the ideomotor approach to action control and learning, which is primarily concerned with the question of how an "idea" (i.e., cognitive representation of an action) can move the body. Action control relies on effect anticipation activating bidirectional action-effect associations that have been acquired through associative learning. Hommel discusses conditions for acquisition and anticipation, the aspects of an action controlled by effect anticipations, and implications of the ideomotor approach for the representation of the agent's self.

Part II: Ecological Approaches

Part II presents ecological approaches to action and perception. In contrast to the more cognitive approaches of the first part, ecological approaches avoid the notion of mental representations, since it is assumed that all visual information necessary for visually guided action is provided by, and contained within, the environment.

Chapter 6, by Michael Turvey, reviews the ecological perspective on perception and action, including discussions of philosophical and epistemological

foundations and focusing on the question of how organisms make their way in the world. Aiming to explain agency as a property of all organisms, Turvey presents a framework founded on physics, namely, on the laws of thermodynamics. One central principle of the ecological perspective is that the organism's environment consists of possibilities for action (*affordances*) and is perceived as such. Moreover, the environment is dynamic in that it continuously changes through movements of the organism, necessitating a dynamic analysis of perception-action cycles.

In chapter 7, Dennis Proffitt and Sally Linkenauger present an embodied approach to visual perception. More specifically, they argue that visual information is scaled by nonvisual aspects of the individual's body (consisting of three attributes: morphology, physiology, and behavior) that are relevant to the execution of purposive action. Accordingly, perception entails an interaction between the selected environment, the actor's body, and the actor's purposes, with the actor's purposes determining the organization of the body, which in turn determines the aspect of the body that is used as a perceptual ruler. The second part of the chapter presents empirical support showing that distances in near space are scaled by morphology, whereas the spatial layout of large environments, like the steepness of a hill, is scaled by physiology. Moreover, evidence suggests that for target-directed actions, the apparent sizes of the targets are scaled by behavioral performance.

Part III: Neurocognitive Mechanisms

Part III focuses on the neurocognitive mechanisms involved in action understanding and the close coupling of attention and action.

Chapter 8, by Giacomo Rizzolatti and Corrado Sinigaglia, reviews the brain mechanisms that are assumed to underlie immediate and direct action understanding, that is, understanding of the observed action as one's own motor possibility. Based on the discovery of "mirror neurons" in the monkey's premotor cortex discharging both during action observation and execution, it is argued that direct action understanding relies on the activity of brain areas transforming sensory representations of observed actions into a motor format (i.e., the mirror mechanism). The authors start by reviewing the anatomy of the parieto-frontal network in nonhuman primates and humans, followed by a review of the basic functional properties of neurons and neural circuits of this network. Finally, they discuss recent data suggesting that the mirror mechanism is critical for perceiving actions of others in terms of both the goal of the action and its specific visual aspects.

In chapter 9, Glyn Humphreys starts from the idea that selection occurs for the sake of successful action, so that only behaviorally relevant objects are selected. He goes beyond this argument, however, suggesting a close interaction between action and attention, in the way that action in turn influences attentional selection. Evidence suggests that action planning influences the way that attention operates. The same holds true for action-related properties of objects in the absence of any plan to act. Humphreys demonstrates that this latter effect is mediated by activation in ventral areas of the cortex, which are associated with object recognition, rather than by dorsal areas classically associated with action. A further sign that attention and action are closely interwoven is given by findings that the attentional response to action-related information in an image is accompanied by an enhanced response within dorsal premotor regions, which are typically associated with motor planning.

Part IV: Development

Focusing on action in infancy, part IV takes a developmental perspective on action science. The two developmental approaches presented address the role of actions in cognitive development, as well as the relationship of action perception and production in infancy.

In chapter 10, Claes von Hofsten suggests that action is the foundation for all aspects of cognitive development. He explains that newborns are already well equipped to perceive and extract physical rules of the external world, to control their own actions, and to be sensitive to social signals. We can infer that they are therefore already prepared to control their actions in a predictive manner. In addition to this preparedness, von Hofsten discusses the motives to explore the world, to move, and to interact as the driving force for the acquisition of knowledge by acting.

Chapter 11, by Andrew Meltzoff, Rebecca Williamson, and Peter Marshall, provides a developmental perspective on the link between action perception and action production focusing on imitation in infancy. The authors review their findings of action imitation already observable in newborns and argue that one's own and others' actions are represented in a supramodal way. They discuss further characteristics of infant imitation like top-down control and social affiliation and conclude with a neuroscientific view on the link between action perception and production.

Part V: Social Actions

Part V explores social perspectives related to the study of human actions arising from research on imitation and joint action.

Chapter 12, by Cecilia Heyes, discusses the core mechanisms of imitation on the basis of research on automatic imitation. Automatic imitation is the facilitation or inhibition of a motor response by a similar or dissimilar task-irrelevant action stimulus. Heyes presents two types of alternative models: associative models that claim direct sensorimotor associations between sensory and motor representations of the same action, and conceptual models that suggest that higher-order processing leads from sensory representations to the activation of motor representations. Experimental evidence suggests that processing of the action stimulus, as well as the motor response, can be influenced by experimental manipulations of attention and social factors, respectively, whereas no clear evidence supports the idea that the process of stimulus-response translation can be manipulated. Heyes thus argues that automatic imitation effects are mediated by associative rather than conceptual processes, and concludes by relating associative models of imitation to processes of conditional learning.

In chapter 13, Janeen Loehr, Natalie Sebanz, and Günther Knoblich address the mechanisms underlying joint actions. Such actions are characterized by interpersonal coordination to bring about a change in the environment. The authors suggest that joint actions rely on close perception-action links and shared representations. Perception-action links support coordination in time and allow predictions about the action of one's partner to be made, whereas shared representations guide joint action planning and monitoring. The authors argue that when it comes to joint action, we can fully understand an individual's actions and perceptions only by considering the actions and perceptions of the coactor.

Part VI: Cognition and Volition

The book's final part is dedicated to issues of cognition and volition in the study of human actions. The three approaches presented in this part provide a multifaceted discussion of high-level issues of action science dealing with experience of agency and the relationship between the conceptual system and action, as well as between volition and action.

In chapter 14, Valerian Chambon and Patrick Haggard ask how the experience of agency comes about. They first illustrate why they regard the classical ideomotor theory and newer computational models of motor control as insufficient for explaining the sense of agency, arguing that these accounts neglect the process of action selection. Subsequently they present a thought experiment to depict how the sense of agency is linked to the action selection process. The authors propose a premotor account

that incorporates the action selection process as a transformational link between intentions and performed actions. They also consider the relation between action selection and responsibility.

In chapter 15, Markus Kiefer and Lawrence Barsalou claim that cognition is invariably grounded in perception, action, and internal states. To present this grounded cognition approach, they center on the conceptual system that contains knowledge about the world. They illustrate that both concrete and abstract concepts can be regarded as modal representations referring to sensorimotor experience. Following a theoretical analysis of the explanatory value of grounded cognition theory and the discussion of its challenges, they offer experimental evidence testing specific predictions using multiple methods.

Finally in chapter 16, Thomas Goschke addresses the intriguing question of how voluntary actions are determined. He argues for a view of intentions not as direct triggering causes of actions but as internal constraints biasing perceptual processing and response selection over extended durations. In contrast to the actions analyzed in part I, this perspective thus considers actions on a broader timescale. Goschke subsequently discusses volitional control processes and associated cognitive and neural mechanisms by which intentions are shielded from competing habitual or motivational responses. To address the question of how cognitive control processes themselves are regulated, he concludes by offering a framework in which voluntary actions emerge from interactions between large-scale brain systems mediating complementary control functions.

Where to Go?

As should have become clear by now, researchers have so far progressed along diverse trails through the landscape of action science and accordingly have arrived (or taken a rest) in different districts; sometimes these places are at least adjacent to each other, and sometimes they are far apart. Likewise, researchers differ in their style of traveling.

At first sight, one may call this methodological and theoretical diversity of approaches a disadvantage, turning the field mapping of action science into a Sisyphean task. However, this diversity may turn out to be a challenge, as well as a great chance for a fledgling discipline. Similar to evolution, which depends on genetic diversity, a new emerging field in science depends on a rich and multifaceted supply of theoretical and methodological approaches, some of which are still waiting for their mettle to be tested. Accordingly, in the field's present state, two general lines of thought have

evolved regarding the way action science should proceed: either one may strive for a *unification* of approaches, or one may seek to cultivate their *diversity*.

Whatever one's preferred option—unification or diversity—ironically, acting on the further development of action science (as well as on any other newly emerging field of research) might be called an incredibly bad example of voluntary action: criteria for the description of the final goal are lacking, and there is also no clear assignment of an action (in terms of concrete scientific activity) leading to the goal. However, eventually, it is not for nothing that the concept of "searching" is inherent in the term "research."

After all, the lack of a precise map for the landscape of action science bears an enormous advantage: scientific activity can be guided by the driving forces of curiosity and exploratory spirit. Finally, we must keep in mind that when drawing a map of a landscape, the more trails and districts (and also detours and blind alleys) are known, the better the map will be. *Action Science: Foundations of an Emerging Discipline* provides the travelogues.

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I Control and Learning

2 Tool Use in Action: The Mastery of Complex Visuomotor Transformations

Herbert Heuer and Sandra Sülzenbrück

Introduction

Humans have extraordinary skills of tool use that exceed those of other primates. A possible reason is that basic sensorimotor learning is supplemented with mechanical reasoning (cf. Johnson-Frey, 2003). In general, tool use is the "use of a functionally unattached environmental object to alter more efficiently the form, position, or condition of or to perceive, or to act directly and physically upon, another object, another organism, or the user itself when the user holds or carries the tool during, or just prior to, use and is responsible for the proper and effective orientation of the tool" (Holmes, Sanabria & Calvert, 2007). This chapter examines the use of a subset of tools of a certain level of complexity that perhaps requires some mixture of elementary associative learning and higher-level processes. Prototypical of the tools we have in mind are those used in minimally invasive or laparoscopic surgery (cf. Gallagher, McClure, McGuigan, Ritchie & Sheehy, 1998).

Laparoscopic tools can formally be described as first-order levers with a variable fulcrum and thus variable lengths of load arm (with the effective part of the lever as the tip of the load arm) and effort arm (with the hand holding the proximal end of the effort arm). Figure 2.1a illustrates such a device, which is similar to those used in several of the experiments reported here. In the experiments, the lever itself was invisible, and the position of its tip was represented by the position of a cursor on the monitor. For any tool, the transformation of the bodily movements, mostly of the hand controlling the tool, into the resulting movements of the effective part of the tool is the kinematic transformation. The kinematic transformation of a lever is the transformation of the positions of the hand in the positions of the tip of the lever or, equivalently, in the representation of the position of this tip (typically a cursor) on the monitor. Figure 2.1b illustrates the

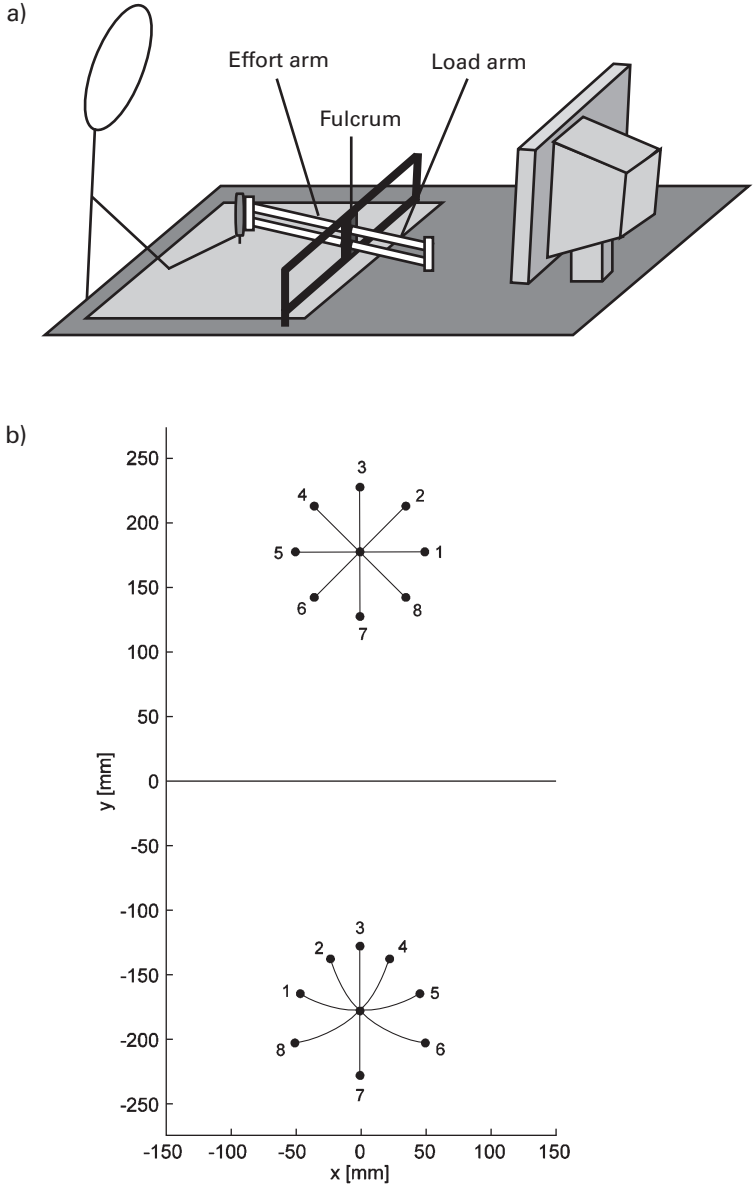

Figure 2.1

(*a*) Sketch of a two-sided lever. In experiments the hand and the lever are invisible, and the position of the tip of the lever is presented on the monitor. (*b*) Target positions of the tip of the lever with straight trajectories (*upper part*) and the associated positions of the hand (*lower part*) for movements from a central start location to eight different targets.

kinematic transformation for movements from a central start position to eight different targets. For the cursor (or the tip of the lever), straight paths are shown. The corresponding paths of the hand are curved, the directions of hand movements differ from the directions of cursor motions, and so does their amplitude.

The kinematic transformation of the sliding lever can be characterized in a more general way than for particular movements, as illustrated in figure 2.1b. For pure sliding movements, the tip of the lever moves in the same direction as the hand and by the same distance. The complications come about through the rotations of the lever. For rotations there is a left-right inversion, which is also called the fulcrum effect. In addition the gain, that is, the relation of the amplitudes of cursor and hand movements, depends on the relative lengths of load arm and effort arm. The relatively longer the load arm is, the higher is the gain. When one analyzes movements in different directions, which represent combinations of sliding and rotating the lever, the gain depends on direction. This is called gain anisotropy. The particular shape of gain anisotropy depends on the position. All in all, this is a quite complex kinematic transformation (see Heuer & Sülzenbrück, 2009, for details) that should be difficult to master.

The use of complex tools or the mastery of complex visuomotor transformations can be studied both from an applied and from a basic-research perspective. In this chapter we take the second perspective and address six issues in turn: accuracy, transparency, awareness, aging, distality, and embodiment. What each of these labels actually hides may not be immediately obvious but will become clearer later on. Before we discuss these issues, we briefly introduce some basic concepts.

Control and Ideomotor Action

The mastery of a transformation can be viewed as a problem of control. There is some system such as a tool, and the goal is to achieve a certain output. This requires the identification of the appropriate input. In principle, control problems can involve various levels of complexity, depending on the kind of system to be controlled. This can be a mechanical tool, but it can also be a social system (cf. Wolpert, Doya & Kawato, 2003).

Control problems can be solved in two principally different ways, which are combined in human motor control (cf. Cruse, Dean, Heuer & Schmidt, 1990; Heuer & Massen, in press; Jordan, 1996). The first solution is closed-loop (or feedback) control. It is feedback based, and the input of the transformation is more or less continuously modulated to reduce the error, the

deviation of the actual output of the transformation from the desired output. The second solution is open-loop (or feed-forward) control. Here the appropriate input is estimated directly from the desired output, which requires knowledge of the transformation. The internal representation of the transformation is often referred to as an internal model (Heuer, 1983; Wolpert & Kawato, 1998).

The notion of control bears an obvious similarity to the concept of ideomotor action, which has a much longer history (Stock & Stock, 2004). Both notions share the claim that action selection starts with the desired effects. Control theory focuses on the question of how the movements that are needed to produce the desired effects are determined, whereas ideomotor theory takes the step from the intended effect to the appropriate movement as given (cf. Heuer & Sülzenbrück, 2012). Consistent with this difference, the transformations used in studies of ideomotor theory are quite simple, mostly with binary input and output signals (cf. Beisert, Massen & Prinz, 2010; Hommel, Müsseler, Aschersleben & Prinz, 2001; Hommel, 2009; Massen & Prinz, 2009). They can be conceptualized as simple associations that can be used bidirectionally to derive either the expected effect of a given movement or the movement required to produce a desired effect. However, even with these simple transformations, chronometric studies reveal that different transformations require different times to determine the movements needed for a certain effect (e.g., Kunde, 2001; Kunde, Müsseler & Heuer, 2007; Müsseler, Kunde, Gausepohl & Heuer, 2008). Control theory, in contrast, deals with more complex transformations, which are generally defined for continuous input and output variables, often multidimensional ones. In this case the derivation of the required input from a desired output is no longer trivial, for example, for the complex visuomotor transformations considered in this chapter.

The Issue of Accuracy

According to Fuchs (2002), minimally invasive surgery has two drawbacks: a prolonged learning phase and an increased operation time. The prolonged learning phase is related to the difficulty of the tool used. The increased operation time is related to the incomplete learning of the transformation. When the internal representation of the transformation is only an approximation, but accurate performance is required, this puts a heavy load on visual closed-loop control. Both experimental data and theoretical considerations suggest that the slow performance with a complex tool such as a sliding lever is indeed due to the requirement of closed-loop control.

Sülzenbrück and Heuer (2011) compared movement time of aimed movements with a virtual sliding lever during practice with continuous and terminal visual feedback. With a virtual sliding lever there is no physical lever, but the transformation of hand movements into cursor motions works exactly as it does for a real lever. Thus there is the corresponding visuomotor transformation, but not the variable resistance of the lever. With concurrent visual feedback, the cursor is presented during the movement so that closed-loop control is possible. With terminal visual feedback, in contrast, the cursor is presented only after the movement has ended. Thus visual closed-loop control is impossible, but the error shown at the end of the movement can be used to update the internal representation of the transformation. With terminal visual feedback, movement time was in the order of 2 seconds and changed only little in the course of practice. With concurrent visual feedback, movement time was about twice as long at the end of practice, and initially even about three times as long. These large differences are certainly due to the demanding task. With a proportional transformation of hand movement to cursor motion, the effect of concurrent visual feedback is less, but it is still present (e.g., Chua & Elliott, 1993).

Why does the requirement of processing visual feedback produce such slow movements? Visual closed-loop control suffers from processing delays (cf. Heuer & Massen, in press). Such delays enhance the risk that control becomes unstable, in particular when the gain of the loop is too high. Therefore the gain must be small, and as a consequence movements will be slow.

In the course of practice, movement times declined considerably in the concurrent-feedback condition of Sülzenbrück and Heuer (2011). There are at least two reasons for this. First, processing delays tend to become shorter in the course of practice, and this is accompanied by a higher gain of closed-loop control, so that the corrective movements, given certain errors, become faster (cf. Pew & Rupp, 1971). Second, the load on visual closed-loop control is likely to decline because the internal representation of the visuomotor transformation becomes more accurate. The accuracy of the internal representation can be determined in trials without visual feedback (cf. Davidson, Jones, Sirisena & Andreae, 2000; Heuer, 1983). The more accurate the internal representation is, the smaller are the errors that remain to be corrected by way of processing visual feedback.

What are the characteristics of the internal representation of the complex visuomotor transformation of a sliding lever? Figure 2.2 shows averaged trajectories of the hand and of the cursor in an open-loop test

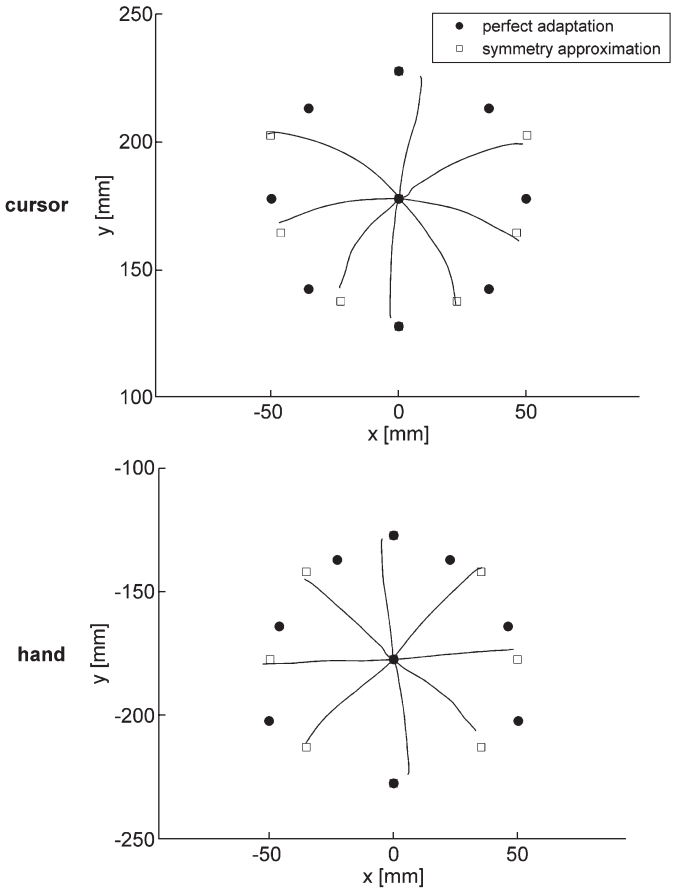

Figure 2.2
Averaged movement trajectories of the cursor (*upper part*) and the hand (*lower part*) during open-loop tests with a virtual lever. Targets of the lever transformation are shown as filled circles; targets of the symmetry approximation are marked by open squares (after Sülzenbrück & Heuer, 2009a).

with a virtual sliding lever (Sülzenbrück & Heuer, 2009a). With a physical lever and after practice with a physical rather than a virtual lever, the results were quite similar. In terms of accuracy, these movements were clearly inaccurate. However, the errors were not just random but highly systematic. Rather than at the targets presented (filled circles for the cursor; the filled circles for the hand indicate the associated positions of the hand), the movements ended close to other locations that are marked by open squares. These locations correspond to the target positions if a simplified approximation of the complex visuomotor transformation of the sliding lever had been learned instead of the actual lever transformation. We refer to this approximation as a symmetry approximation.

The symmetry approximation works as follows. Let (x_t, y_t) be the coordinates of a target in a Cartesian frame of reference centered in the start location of the cursor with a horizontal abscissa. Then the hand target is chosen as (x_h, y_h) with $x_h = -x_t$ and $y_h = y_t$ in a Cartesian frame of reference centered in the start location of the hand with a frontoparallel abscissa. Thus the hand target is the line-symmetric cursor target in a shifted frame of reference. This symmetry approximation is consistent with the observation of Abeele and Bock (2001) that for adaptation to visuomotor rotations of more than 90°, the initial adjustment is a point-symmetric movement, corresponding to a rotation of 180°. According to these authors, the point-symmetric movement is only a first step in the adjustment to a visuomotor rotation of more than 90°. It is followed by a gradual reduction of the rapid (over)adjustment of 180°. In contrast, the data of figure 2.2 seem to suggest that the symmetry approximation not only is a first step in the acquisition of an internal representation of the visuomotor transformation but is all of what is learned. The most likely reason is that during practice, continuous visual feedback was available.

With continuous visual feedback during practice, accurate movements can be produced even without an accurate internal representation of the visuomotor transformation. What can be gained by an accurate representation is only some savings of movement time, and when a rough approximation such as the symmetry approximation results in movements that are sufficiently close to the targets, the possible savings of movement time are small. The situation is different when the symmetry approximation produces larger errors with a certain set of targets, and in particular when visual feedback is not continuously presented during practice trials. In fact, some visuomotor transformations are not learned with continuous visual feedback during practice, but are learned with terminal visual feedback that shows only the deviation of the final position of the movement from the

target (Heuer & Hegele, 2008a). Acquisition of a more precise internal representation with terminal than with continuous visual feedback has also been shown for the sliding lever (Sülzenbrück & Heuer, 2011). In fact, with terminal-feedback practice, a gradual shift of the symmetry approximation to a more precise internal representation of the visuomotor transformation can be observed (Sülzenbrück & Heuer, 2010).

From these findings, one can tentatively conclude that the acquisition of a representation of the transformation of bodily movements into movements of the effective part of a complex tool is likely the result of an interplay of two qualitatively different processes. According to this claim, a rough approximation of the transformation is acquired in a first step. It is shaped by the most prominent features of the relation between hand movements and movements of the tip of the tool. In the case of the lever transformation, the most prominent feature is the left-right inversion. Explicit knowledge of the visuomotor transformation of the lever seems to be restricted to this first process. Only when the approximation, that is, the result of the first process, is too inaccurate and results in too large endpoint errors, or when participants cannot rely on closed-loop control, is the second process initiated. It is characterized by a slow and gradual approach to an accurate representation and thus to the actual hand-target positions of the lever transformation. The two-process hypothesis is in line with other research showing that motor learning can proceed in progressions of approximations (Koh & Meyer, 1991; Abeele & Bock, 2001).

As the data presented here indicate, complex visuomotor transformations are not necessarily associated with complex internal representations. Rather, internal representations can be relatively simple approximations, or perhaps all control might remain closed loop, resulting in slow movements. Only when they result in sufficient benefits will internal representations beyond simple approximations be acquired. Thus a kind of resistance works against the acquisition of more accurate representations. As a consequence of this adaptive inertness, errors in the end positions of movements are likely not to be random but to systematically point to the simplified approximations involved.

The Issue of Transparency

Visuomotor transformations can be defined in fairly arbitrary ways. This is obvious for the relation between hand movements and cursor motions. The increasing flexibility of designing transformations invades other sectors of our everyday life as well, for example, when we drive a car with

advanced steering gears. Mechanical reasoning is likely to be of little help in mastering such devices because there are no mechanisms from which the user could derive the nature of the transformation. However, mechanical reasoning might be important for the mastery of visuomotor transformations that obey the rules of some mechanical system, whether or not the mechanical system is actually used to implement them. Of course, the user should be aware of such a system, either by way of seeing it or by way of imagining it.

For the case of a sliding lever, it has been shown that performance (in terms of movement time) in a simulated laparoscopic task can be improved by showing a part of the instrument on the monitor (Wentink, Breedveld, Stassen, Oei & Wieringa, 2002). The same observations have been made with simple pointing tasks, for which movement time was slower when only the cursor was presented on the monitor than when the load arm of the lever was depicted in addition (Sülzenbrück & Heuer, 2012). The load arm was illustrated by a line that emanated from a fixed position at the bottom of the monitor and ended in the cursor position. The beneficial effect of an increased mechanical transparency on movement time was particularly pronounced at older working age (Heuer & Hegele, 2010).

Whereas the beneficial effects of the visible load arm of the sliding lever on performance are clear, its effects on the acquisition of an internal representation of the visuomotor transformation are less obvious. On the one hand, one could expect that a higher level of transparency supports the acquisition of an internal representation. For example, imagery of a sliding lever could help in assigning a position of the tip of the lever to a certain position of the hand. However, the presentation of the load arm of a sliding lever can also be conceived as a kind of environmental support. Environmental supports are useful because they typically mitigate age-related declines in performance (Charness, 2008; Morrow & Rogers, 2008), but they do so because they serve as substitutes for internal representations. In the longer run, performance might actually become dependent on the environmental support. Thus, rather than boosting the acquisition of an internal representation of the visuomotor transformation, the enhanced transparency by additional visual information could also impede it.

Empirical evidence for negative effects of mechanical transparency on the acquisition of an internal representation comes from a study in which participants practiced with a physical lever (Sülzenbrück & Heuer, 2012). Although during practice mechanical transparency led to better performance in terms of shorter movement times, the internal representation of the visuomotor transformation in terms of end-point accuracy in open-loop

tests was worse after practice with the visible load arm. In contrast, in another study, the accuracy of the internal representation of the visuomotor transformation was not affected by enhanced mechanical transparency during practice (Heuer & Hegele, 2010). In the latter study, the sliding lever was virtual rather than physical, but it is not evident why this difference should result in different effects of mechanical transparency on the acquisition of an internal representation of the visuomotor transformation.

As far as the issue of transparency is concerned, the available data on the acquisition of an internal representation of the visuomotor transformation are not conclusive. In addition, different means to enhance transparency could produce different results. In spite of several open questions, the available data strongly suggest that closed-loop performance can be improved by a visible part of the tool. Perhaps the visible load arm in the studies reported makes the left-right reversal for rotations of the lever particularly conspicuous. This would fit to previous observations on tracking with a visible steering wheel that can be useful to improve performance with a transformation that implements a pure right-left reversal (Merz, Kalveram & Huber, 1981). When grasping the steering wheel at the bottom, a leftward movement of the hand is transformed into a rightward movement of the top of the wheel, which matches the rightward movement of the target. The visibility of the steering wheel serves to enhance performance in the tracking task, as opposed to a condition where the steering wheel is invisible.

The Issue of Awareness

The acquired internal representation of a visuomotor transformation can be subject to conscious awareness or not, and between awareness and lack of awareness there can be intermediate states. To distinguish between implicit and explicit knowledge of the transformation, we reserve the term "internal model" for the implicit component of the representation, and we refer to the explicit component as "explicit knowledge." Adjustments can be based on both the internal model and the explicit knowledge. Whereas for the internal model we assume a direct link to corresponding motor adjustments, because the model is part of open-loop control, for explicit knowledge the link to corresponding strategic adjustments is looser. Explicit knowledge is a prerequisite for strategic corrections, but we also cite examples for explicit knowledge that is not used to enhance performance (e.g., Kleinsorge, Schmidtke, Gajewski & Heuer, 2003; Shanks & Cameron, 2000).

When one thinks of visuomotor transformations as implemented by a sliding lever, or of less complex transformations such as visuomotor rotations (cf. Cunningham, 1989), it seems hard to believe that one should not become aware of the discrepancies between hand movements and cursor motions. On the other hand, in everyday life one seems not to be aware of one's hand position when one controls the position of the cursor on a computer monitor. Perhaps it is visual capture that contributes to the poor awareness of discrepancies between felt and seen positions of hand and cursor (cf. Welch, 1978, p. 44).

Müsseler and Sutter (2009) studied more formally whether participants were aware of their hand movements during control of the motion of a cursor. Their participants were instructed to move a cursor on a circular path on a monitor by way of appropriate hand movements. These hand movements also had a circular path when the visuomotor gains for the x and y axes were identical. However, when the gains were different, participants had to draw an ellipse to produce a circular path of the cursor. These ellipses could be elongated along one or the other axis. Participants had to judge the orientation of the ellipse. The accuracy of these judgments indicated whether participants were aware of their hand movements, in particular of the eccentricity of their elliptical path. For 50 percent accuracy, a ratio of the longer to the shorter axis of the ellipse of more than 1.5 was required. The limited awareness of the hand movements implies a limited awareness of the transformation, for which the hand position is the input variable and the cursor position the output variable. As Müsseler and Sutter (2009) pointed out, the low level of awareness may actually support tool use in that interference from the experienced discrepancies between movements of the hand and cursor motions is avoided.

Explicit knowledge of the visuomotor transformation can be used for intentional (or strategic) corrections such as side pointing or past pointing. For example, knowing that the visuomotor gain is less than 1 (meaning that a hand movement of a certain amplitude would result in a smaller amplitude of movement of the end effector), one can produce a movement that is intended to end at a position beyond the target. Or knowing that the sliding lever requires a left-right reversal, one can move the hand to a symmetrical location. Such intentional corrections have been shown to coexist with implicit adjustments to novel visuomotor gains. In fact, some evidence indicates that these adjustments are functionally independent (Sülzenbrück & Heuer, 2009b; Taylor, Klemfuss & Ivry, 2010). In the extreme case, a perfect intentional correction can be added to a gradually developing implicit adjustment so that the total adjustment results in an

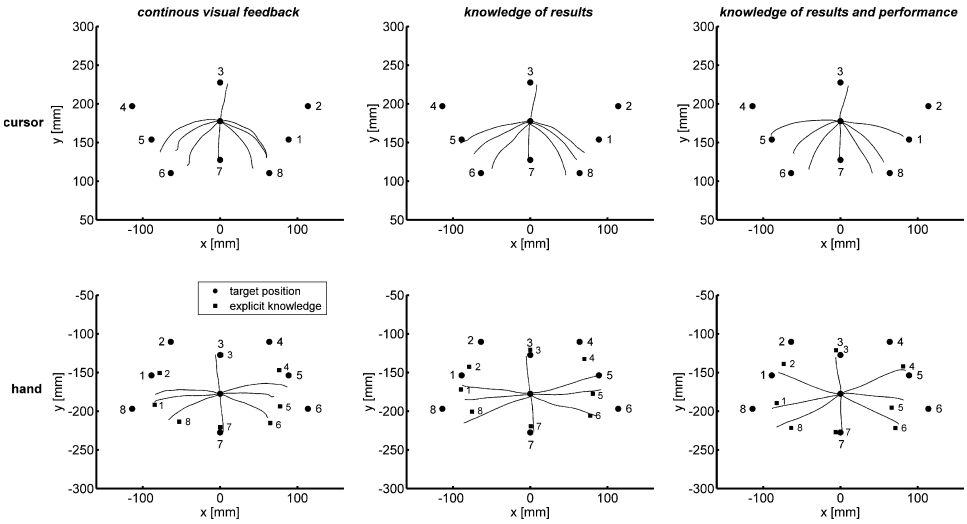

Figure 2.3

Averaged movement trajectories of cursor (*upper part*) and hand (*lower part*) during open-loop trials after practice of the kinematic transformation of the virtual lever with different types of visual feedback (continuous visual feedback, knowledge of results, knowledge of results and performance). Black filled circles represent target positions of the lever transformation in cursor space and hand space; gray squares represent explicit knowledge about the hand positions associated with equally numbered targets on the screen (after Sülzenbrück & Heuer, 2011).

overcompensation of a visuomotor rotation (Mazzoni & Krakauer, 2006). However, in the shorter or longer run, the intentional correction may also be modified or abandoned (Hegele & Heuer, 2010a; Taylor & Ivry, 2011).

What is the explicit knowledge about the visuomotor transformation of the sliding lever? Figure 2.3 displays mean movement trajectories of the cursor and the hand in open-loop trials after practice of the visuomotor transformation of the virtual lever for three experimental groups differing in the type of visual feedback during practice (Sülzenbrück & Heuer, 2011). Although movements did not reach the target positions (filled black circles) accurately, the left-right inversion from hand to cursor movements was taken into account. The explicit knowledge about the target positions of the hand is displayed as gray squares, which represent the mean explicit judgments of the hand targets for given visual targets indicated by the numbers in the figure. Explicit knowledge was assessed by asking participants to report the locations of the hand that were associated with target

positions of the cursor presented on the monitor. The reported hand positions were read from a coordinate system placed on the opaque screen that shielded the hand and the lever from view. Generally, explicit judgments about the target positions of the hand were inaccurate, both with respect to the correct hand targets and with respect to the end points of the hand movements. However, the inverse relation of hand and cursor movements was always taken into account.

The Issue of Aging

Adjustment to the complex visuomotor transformation implemented by a sliding first-order lever suffers at older working age (Heuer & Hegele, 2009). Under closed-loop conditions, movement time was faster for the younger adults than for the older ones, and this difference increased in the course of practice. In open-loop tests, the internal representation of the transformation turned out to be less accurate for the older than for the younger participants on the average. However, this difference in the means resulted from a larger number of older participants with almost no adjustment at all and a smaller number of older participants with almost perfect adjustment. The observation that the age-related variation of adjustment was due to the relative frequencies of different categories of the quality of adjustment and not to a graded variation can be taken to suggest that it was related to the presence versus absence of explicit knowledge. This hypothesis is in line with a number of findings according to which at older age the acquisition of explicit knowledge of a (sufficiently complex) visuomotor transformation is impaired, whereas the acquisition of implicit knowledge or of an internal model is unaffected at least up to age 65.

When younger and older adults are compared with respect to their adjustment to a visuomotor rotation, which is a less complex transformation than the one implemented by the sliding lever, typical findings have been obtained several times (Bock, 2005; Bock & Girgenrath, 2006; Buch, Young & Contreras-Vidal, 2003; Heuer & Hegele, 2008b; McNay & Willingham, 1998). First, the internal representation of the transformation is less accurate in the older adults than in the younger ones. Second, studies show no age-related variation of aftereffects. Aftereffects are changes of pointing that remain after the practice period although the visuomotor transformation is no longer present. The difference between these two tests had been hypothesized to result from the contribution of explicit knowledge to visual open-loop performance in the presence of the transformation, but not in its absence (aftereffects). When additional tests of explicit

knowledge were performed, these revealed the corresponding age-related variation (e.g., Bock, 2005; Heuer & Hegele, 2008b). This pattern of results has been observed not only with visuomotor rotations but also with direction-dependent changes of the visuomotor gain (Hegele & Heuer, 2010b).

The age-related variation of explicit knowledge, but not of implicit knowledge, has consequences. Among them is the capability of dual adaptation, that is, of the concurrent adaptation to different transformations. There are conditions under which dual adaptation is impossible, for example, when only sequential order determines whether the one or the other transformation is in effect (e.g., Karniel & Mussa-Ivaldi, 2002). On the other hand, there are conditions that enable dual adaptation. For example, dual adaptation is possible when the one transformation is effective in one region of the workspace and the other transformation in another region (Woolley, Tresilian, Carson & Riek, 2007). Different regions in the workspace typically mean different regions for hand movements and different regions for target presentation and visual feedback. However, when target and feedback are presented on a monitor, one will ask whether the difference in visual space or motor space is what enables dual adaptation.

Hegele and Heuer (2010c) studied dual adaptation to visuomotor rotations in opposite directions with different start positions of the cursor, but not of the hand. Whereas the younger participants acquired different internal representations, depending on the visually perceived start location, the older participants acquired no internal representations of the opposite visuomotor rotations at all. This pattern of results was matched by the explicit shifts, whereas aftereffects were absent in both age groups. This suggests that without movements in different regions of the workspace and only visual cues for the type of transformation, dual adaptation is mediated by explicit knowledge. As far as the acquisition of an internal model is concerned, the adjustments to opposing visuomotor rotations cancel each other out.

The findings reviewed could leave the impression that the age-related variation of explicit shifts is causal for the age-related variation of the accuracy of internal representations as revealed in visual open-loop tests. This impression is likely to be wrong. Although age-related variations mostly, but not always, disappear when age groups are matched by explicit knowledge (Heuer & Hegele, 2008b), the existing evidence is only correlative. Preliminary attempts to boost explicit knowledge in particular of older persons have not simply made the age-related variations disappear. Thus the relation between explicit knowledge and performance in open-loop tests may be more complicated than initially thought. Perhaps older adults not only acquire less explicit knowledge but also are at higher risk of not using such knowledge for behavioral adjustments to the visuomotor transformation.

The Issue of Distality

When humans use a complex tool such as a sliding lever, they produce coupled movements of their hand and of the tip of the lever at the same time. Which of these movements is primary in terms of planning and control, and which is just a mechanical (or electronic) consequence of the other? With respect to the sequence of signals and transformations involved in motor control (cf. Heuer & Massen, in press), the hand movement is more proximal, and the movement of the tip of the lever is more distal. Thus we ask: is the proximal movement controlled and the distal one just a mechanical consequence, or is the distal movement controlled and the proximal one organized in a way that certain characteristics of the distal movement result?

A similar issue has been addressed with respect to joint movements and movements of the end effector, and the general conclusion has been that motor planning and control refer to end effectors (e.g., Atkeson & Hollerbach, 1985). Here we extend this question to the use of a tool. Perhaps those characteristics of hand movements that are present without a tool will become characteristics of movements of the effective part of the tool. This would be the signature of distal control. Alternatively, and signifying proximal control, the hand movements would maintain their characteristics. Without tool use an important characteristic of aimed movements is their (almost) straight path (e.g., Abend, Bizzi & Morasso, 1982; Kaminski & Gentile, 1986; Morasso, 1981).

The upper part of figure 2.4 shows the approximately straight paths of the cursor and thus of the tip of the sliding lever, both with a physical and a virtual lever. Of course, the associated paths of the hand, displayed in the lower part of figure 2.4, are curved. The same kind of observation has also been made for other transformations that transform straight hand movements into curved cursor motions (Flanagan & Rao, 1995; Goodbody & Wolpert, 1999; Wolpert, Ghahramani & Jordan, 1995). Thus one might conclude that motor control and motor planning are distal. However, these findings are restricted to visual closed-loop conditions.

Averaged movement paths under visual open-loop conditions are shown in figures 2.2 and 2.3. There the paths of the hand are approximately straight, and the paths of the cursor are curved. This is the typical observation under open-loop conditions for the virtual lever. Thus curvature of the hand paths results not from the internal model of the visuomotor transformation or from explicit knowledge but from closed-loop control. Only when the cursor is visible does the visual perception of straightness or curvature dominate the perception of the hand path. The dominance of

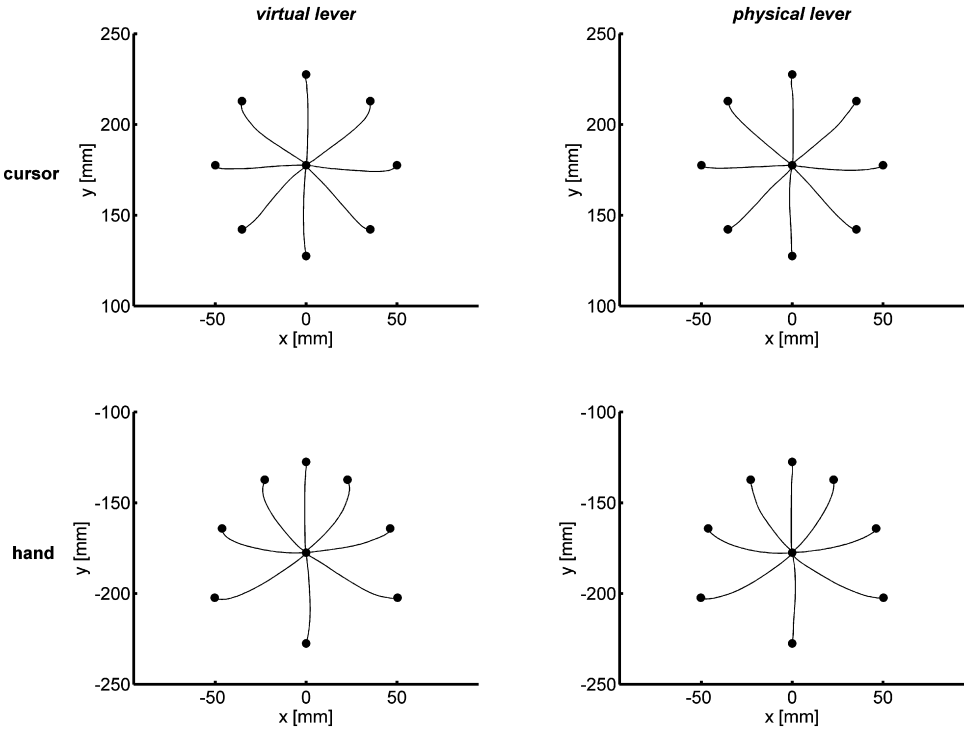

Figure 2.4
Averaged trajectories of cursor and hand movements during closed-loop practice trials for groups either using the virtual lever (*left*) or the physical lever (*right*). In both groups, movements of the cursor were almost straight, whereas the associated hand movements were curved (after Sülzenbrück & Heuer, 2009a).

visual information, when it is available, is reminiscent of some findings on bimanual coordination. For example, the production of bimanual periodic movements with a phase shift of 90° is quite difficult, but it becomes remarkably easier when visual feedback is added such that the position of the one hand is displayed horizontally and the position of the other hand vertically (Swinnen, Lee, Verschueren, Serrien & Bogaerds, 1997). With a phase shift of 90°, the cursor moves on a circular path, and deviations from 90° result in elongated shapes. Similarly, bimanual rotations with nonharmonic frequencies can be produced when they are mapped on equal-frequency visual feedback (Mechsner, Kerzel, Knoblich & Prinz, 2001).

The observations on the distality of motor control in tool use are consistent with an extension of the vectorial-coding model. According to this

model, direction and amplitude are separately specified and controlled movement parameters (e.g., Bock, 1992; Gordon, Ghilardi & Ghez, 1994; Rossetti, Desmurget & Prablanc, 1995; Vindras & Viviani, 1998, 2002). Vectorial coding, in principle, makes a task such as moving a cursor on a monitor to a target simple: the visual movement vector is transposed such that its origin is shifted from the visual start position to the start position of the hand. When the hand movement is mapped on cursor motion 1:1, the visual vector corresponds to the movement vector. Otherwise it has to be transformed according to the internal representation of the visuomotor transformation. Verwey and Heuer (2007) and Rieger, Verwey and Massen (2008) concluded from their data that the internal representation is applied not to the desired trajectory of the movement but to the desired end position; this amounts to rotating and scaling the vector. In their study of nonlinear amplitude transformations, the velocity profile was not distorted by the transformation, similar to the absence of curvature in the open-loop hand movements with the sliding lever. Thus the internal representation is applied only to direction and amplitude of the visual motion to obtain direction and amplitude of hand movement that is then produced as normal—with a straight path. Only when the path is visible does vision become dominant; the path of the cursor becomes straight.

The situation becomes somewhat more complicated when a physical lever is used. In figure 2.4 there is a tendency that deviations from straightness of the cursor path are even smaller with the physical than with the virtual lever. In fact, Heuer and Sülzenbrück (2009) found straighter movements of the tip of the lever than of the hand even under visual open-loop conditions. When Sülzenbrück and Heuer (2010) examined the curvature of hand paths and cursor paths during practice with a virtual and a physical lever, they found essentially straight paths of the hand with the virtual lever, but curved paths with the physical lever. Complementing these observations, the curvature of cursor paths was stronger with the virtual than with the physical lever. Most likely the particular curvature of hand movements with the physical lever, which results in straightened paths of the cursor, is a consequence of mechanical characteristics of the lever, in particular its inertia, which depends on movement direction (inertial anisotropy; cf. Heuer & Sülzenbrück, 2009). A consequence of inertial anisotropy is a discrepancy between the direction of force and the direction of movement.

From the findings reviewed, it is evident that no simple solution exists for the distality issue. In a certain respect, motor control is distal by definition: it is the visual target that is reached by the cursor and transformed

into an appropriate hand movement. However, the path is proximally controlled and straight for the hand. Only when the path of the cursor can be seen is it distally controlled and straight for the cursor. Finally, with a physical lever, the dynamic transformation can serve to produce apparently distal control.

The Issue of Embodiment

With tools we can manipulate objects that would otherwise be out of reach. For a long time, the notion that this functional extension of the body via tools also results in the tool becoming somehow integrated into the representation of one's own body—and in this sense becoming part of oneself or embodied—has been based only on anecdotal evidence. For example, in his work on dioptrics, Descartes ([1637] 1958) described a person using a walking stick as experiencing tactile sensations at the tip of the stick. Head and Holmes (1911) proposed that the ability to localize herself in the environment even extends to the feather on a woman's hat.

A vast body of research addresses the question of whether tools extend the body or are even incorporated into the representation of the body. However, the boundaries between extension and incorporation are blurry (see, e.g., De Preester & Tsakiris, 2009). Empirical evidence for the notion that tools can extend the body comes from the work of Iriki, Tanaka, and Iwamura (1996). They investigated the impact of tool use on neural representations of the peripersonal space, which consists of a region of increased multisensory integration of visual, tactile, and auditory information immediately surrounding the body. In their study, monkeys used rakes to fetch distant food pellets. Doing so, the monkeys showed remarkable changes in the visual receptive fields of parietal neurons integrating visual and tactile information. These receptive fields enlarged along the axis of the used rake and shrunk again when the tool was no longer actively used.

Several studies have shown that tools can be incorporated into the multimodal spatial representation of the body, the body schema. For example, temporal-order judgments were similarly disrupted when stimuli were delivered to crossed drumsticks as when they were delivered to crossed hands (Yamamoto & Kitazawa, 2001). Furthermore, tool use can result in a changed limb representation, which takes the extension via the tool into account. Empirical evidence for this comes, for example, from Witt, Proffitt, and Epstein (2005). They showed that distance estimates became smaller if participants held a stick with which the targets could be reached. Berti and Frassinetti (2000) used a line bisection task to study a patient with hemineglect only in near (500 mm distance), but not in far, space

(1,000 mm distance). They found that when the patient used a stick for this bisection task, hemineglect was also found in far space. No such transfer of hemineglect to far space was found when the patient used a light pen to execute the task. Further evidence that tool use is incorporated into the body schema comes from a recent study by Cardinali et al. (2009). The authors showed that the use of a 40-cm-long mechanical grabber for lifting objects affected the kinematics of subsequent movements of the hand without the tool as if the grabber had increased the represented length of the participants' arm.

In contrast to the now widely accepted notions that tools can enlarge the peripersonal space and in some cases can be incorporated into the body schema (for a review, see Maravita & Iriki, 2004), the question of whether tools are actually felt as being part of the body, which is associated with a sense of ownership of the tool, remains to be elucidated. Although some research addressing this issue exists, the results are inconclusive. This can at least partially be attributed to the fact that the terminology is rather inconsistent (for a discussion of embodiment and ownership, see, e.g., de Vignemont, 2007). So far, clear empirical evidence of experienced ownership of tools remains sparse. As Botvinick (2004) pointed out: "The feeling of ownership that we have for our bodies clearly does not extend to, for example, the fork we use at dinner" (p. 783).

In this section on embodiment, we have referred to studies that used simple tools such as sticks, whereas the rest of our chapter focuses on more complex tools such as the sliding lever. In fact, it seems that the issue of embodiment has been addressed only for comparatively simple tools. It is likely that tools will remain more separated from the body schema the more complex the transformations are that they implement. At least much longer practice periods would be expected for complex tools to become part of oneself. Perhaps a prerequisite would be that mastery relies on purely implicit knowledge, without any contribution of strategic corrections. In any case, the exploration of the boundaries of the potential incorporation of tools into the body schema and a potentially associated feeling of ownership could be an interesting future direction of research on the complex visuomotor transformations described in this chapter.

Concluding Remarks

Primates use tools, but the skilled use of tools with complex transformations of body movements into movements of the effective part of the tool is a unique capability of humans. In contrast to lower primates, only humans display the ability to perceive causal relationships between objects

in their environment (Tomasello & Call, 1997; Johnson-Frey, 2003). This unique ability, which can be broadened to mechanical reasoning, makes human tool use special.

In this chapter, we have addressed some important aspects of the mastery and learning of complex tool transformations. We presented a body of research showing that the acquisition of complex transformations depends crucially on the conditions during practice, especially the type of visual feedback and also the information available about the mechanical properties of the tool. Under some conditions, only rough approximations of the complex transformations are learned. Future research should address whether and, if so, how these differences in the accuracy of the internal representation of the transformations are modulated by the costs and benefits associated with the different types of representation. We also referred to the dominant impact of (desired) distal effects on the control of tools. The finding of only little awareness of proximal effects when using tools could be a sign that this feature is a prerequisite for successful tool use. Furthermore, we addressed age-related differences in the ability to successfully control complex tools, which are likely to be associated with differences in the acquisition and adequate use of explicit knowledge of the transformations. Finally we pointed out that during the use of rather simple tools, such tools may become a part of our body (schema).

The skill of using complex tools not only is based on an internal representation of the transformation but continues to depend on visual closed-loop control. Thus the mastery of such complex movement-effect relations lies well beyond the scope of ideomotor theory. Although the transition from the intention to the corresponding movement may appear automatic and cognitively impenetrable in many cases, a complex set of processes exists in between. In this respect, voluntary action is comparable to perception, where the transition from the optic array to conscious awareness is also well hidden from introspection.

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3 Implicit and Explicit Processes in Motor Learning

Jordan A. Taylor and Richard B. Ivry

Introduction

Executing a movement requires two distinct stages: (1) determining the goal or the desired consequence of the movement and (2) specifying the parameters of the movement. Playing billiards requires selecting which ball is to be pocketed and how to approach the cue ball to achieve this goal. The player may plan to strike the cue ball such that it directly hits the target ball into the pocket, or may opt to bank the target ball off a bumper. Once the approach is selected, great skill is required to properly manipulate the pool cue such that the cue ball is struck at the proper angle and with the right force.

As demonstrated in this example, motor skills require the integrated operation of planning and execution. To begin to understand how the various processes associated with these phases interact to yield successful motor behavior, it is useful to consider their respective optimization functions. Planning processes must be sensitive to outcome variables defined in terms of goals, allowing the system to generate and explore novel strategies that may produce long-term gains, even at the expense of short-term costs. While these factors may also influence execution processes, various lines of research indicate that movement optimization is more focused on minimizing factors such as energy expenditure or motor noise.

Planning and execution processes also tend to differ in terms of awareness. Planning processes are frequently explicit; in our pool example, the player might announce an intention to put the eight ball in the corner pocket. Execution processes are generally more implicit; it may be difficult to teach a novice how to balance the cue stick with the postural hand. This distinction is far from absolute: it seems clear that many processes involved in planning operate implicitly (e.g., biases), and we can certainly be aware of how our execution failed, even without external feedback.

Nonetheless it is useful to keep in mind the distinction between planning and execution when considering the role of awareness in the study of skill acquisition.

In this chapter, we focus on two model tasks: the serial reaction time task (SRT) and visuomotor adaptation. An appealing feature of each of these tasks is that they have goal-selection and movement-execution stages, but with emphasis on different stages as most relevant to the task. In the SRT, goal selection is critical to success, while simple motor execution is less important. In visuomotor adaptation, movement execution is critical to task performance, and goal selection is less emphasized. Researchers have probed and manipulated awareness in experiments with both tasks. We review this literature here, focusing on how these two experimental paradigms offer insight into the functional role of explicit and implicit processes in the acquisition and refinement of goal-directed motor behavior. A key theme in this chapter is to ask whether the manner in which a skill is represented varies as a function of learning under implicit or explicit conditions. Indeed, we conclude with an integrative model of the role of implicit and explicit processes in visuomotor adaptation.

Goal-Driven Learning: Insights from the SRT Task

Sequence learning has proven to be an invaluable tool in examining the contribution of explicit and implicit processes in motor learning. In the SRT task, the participant performs a sequential-choice reaction time task. In the standard task, the stimuli appear at one of four locations, and the participant makes a keypress with one of four fingers to indicate the cued location (Nissen & Bullemer, 1987), responding as quickly as possible (fig. 3.1A). The key manipulation is whether the series of spatial locations are selected randomly or follow a specified sequence. Learning is inferred by the difference in reaction time (RT) on trials or blocks in which the stimuli follow a sequence compared to when they are selected at random. Over time, the participants become faster at responding to predictable events and show a cost in RT when these predictions are violated (fig. 3.1B).

An appealing feature of the SRT task is its simplicity, making it appropriate for studies with both normal and neurologically impaired individuals. Participants need not be instructed that they are to learn a sequence; rather, the RT data provide a measure of the degree of sequence learning. Nonetheless participants may develop partial awareness of the sequence and, in the extreme, reach the point where their RTs anticipate the onset of the stimuli. The degree to which participants gain awareness of the

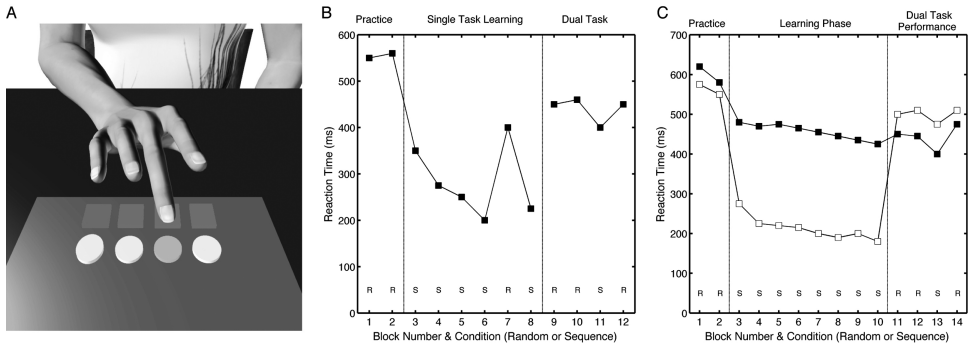

Figure 3.1

(A) Stimuli (LEDs in front of keyboard) appear at one of four locations, and participant presses corresponding key. (B) Single-task condition: the stimuli may be presented at random (R) or follow a repeating sequence (S). Increase in RT on random block after sequence training provides measure of learning. Dual-task condition: addition of a secondary task (e.g., tone counting) results in slower overall RTs and reduced learning effect (compare blocks 8 and 11). (C) White: participants provided with explicit knowledge of sequence prior to the start of SRT training. Black: participants trained under dual-task condition from start of training. During last four blocks, both groups tested under dual-task conditions. Learning, as measured by decrease in RT on block 13, compared to surrounding blocks, is similar for the two groups, suggesting parallel operation of explicit and implicit learning during single-task training. Adapted from figure 1, p. 192, and figure 2, p. 194, from Curran, T., & Keele, S. W. (1993). Attentional and nonattentional forms of sequence learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *19*(1), 189–202, American Psychological Association, reprinted with permission.

underlying sequence can also be experimentally manipulated. Awareness of the sequence may be abolished or attenuated when participants are required to simultaneously perform the SRT task and a demanding secondary task (e.g., discriminate high and low pitch tones that are presented during the response-to-stimulus time interval). Assessing awareness can be tricky (Willingham, Nissen & Bullemer, 1989; Perruchet & Amorim, 1992; Curran & Keele, 1993): postexperimental interviews, in which the participants are asked to either recall the sequence or perform a forced-choice task (e.g., "Press a key indicating where the next stimulus would occur"), are generally used. Even when awareness by these measures is near chance level, sequence learning is evident, although to a lesser degree than under single-task training (Nissen & Bullemer, 1987). The degree of dual-task attenuation (fig. 3.1B) is related to a variety of factors such as sequence

complexity (Cohen et al., 1990) or the temporal relationship between the SRT stimuli and the secondary stimuli (Hsiao & Reber, 2001).

A key debate in the SRT literature concerns the overlap of implicit and explicit learning. Behaviorally, one might suppose that implicit learning reflects the formation of relatively weak stimulus-response associations; gaining explicit awareness of the sequence provides a means to rapidly strengthen these associations. Alternatively, implicit and explicit learning may involve relatively independent processes. Curran and Keele (1993) explored this question by providing a group of participants with knowledge of the sequence before the start of SRT training. As expected, RTs were very fast. However, when a secondary task was introduced after training, performance became similar to a group trained under dual-task conditions from the start (fig. 3.1C). This result suggests the parallel operation of explicit and implicit learning systems: while learning occurred within both systems during training for the informed group, only the implicit system could continue to operate when the secondary task was introduced. Conversely, participants who initially learned under dual-task conditions showed marked improvements when the secondary task was removed; indeed, they performed similarly to participants trained under single-task conditions.

The parallel operation of explicit and implicit learning is also borne out at the neural level. Grafton and colleagues (Grafton, Hazeltine & Ivry, 1995; Hazeltine, Grafton & Ivry, 1997) used PET while participants performed the SRT task with and without a secondary task. When attention was distracted, awareness was minimal, and learning-related changes were prominent in intraparietal cortex, supplementary motor cortex, and motor cortex. In contrast, during single-task training, learning-related changes were correlated with increased activity in prefrontal cortex (PFC), premotor, and the temporal lobe. Within this condition, some participants developed awareness of the sequence. The study showed minimal activation differences in learning-related areas between the aware and unaware participants. Other neuroimaging studies of sequence learning without distraction have identified learning effects in similar networks (Rauch et al., 1995; Doyon et al., 1996; Seidler et al., 2005). These results suggest that whereas implicit sequence learning involves an increase in activation in motor regions, explicit sequence learning involves the recruitment of a network associated with a range of attention-demanding tasks.

Studies of patient populations provide a direct assessment of the neural regions associated with implicit and explicit learning. The classic work with HM (Corkin, 1968), a patient who underwent a bilateral temporal lobec-

tomy, demonstrated that skill learning is preserved in the face of a severe disruption of declarative memory. This dissociation has been confirmed in subsequent work involving amnesiac patients suffering from a range of disorders and pathologies affecting the medial temporal lobe (MTL) region (Corkin, 1968; Weiner, Hallett & Funkenstein, 1983) or pharmacological studies that induce transient amnesia (Nissen et al., 1987). These individuals may exhibit retention of sequence learning over extended periods, despite having no episodic memory of ever performing the task (Nissen & Bullemer, 1987; Nissen et al., 1988). Thus SRT learning does not require declarative knowledge or awareness of the sequence, nor does it require the involvement of neural regions associated with the formation of declarative memories.

Conversely, impairments in SRT learning have been observed in patients with lesions of subcortical structures associated with implicit skill learning and automatization (Phillips & Carr, 1987; Saint-Cyr, Taylor & Lang, 1988; Pascual-Leone et al., 1993; Doyon et al., 1997). Patients with Parkinson's disease or focal basal ganglia lesions exhibit a range of performance on the SRT task, with some studies suggesting a severe impairment (Jackson et al., 1995), and other studies reporting modest degrees of learning (Pascual-Leone et al., 1993; Doyon et al., 1997). The effects of cerebellar pathology are more pronounced. These individuals have been shown to exhibit essentially no evidence of sequence learning (Pascual-Leone et al., 1993; Doyon et al., 1997; Shin & Ivry, 2003).

However, one recent study suggests that the cerebellum may not be related to sequence learning per se but may be involved with the maintenance of the S-R associations (Spencer & Ivry, 2009). In most sequence-learning paradigms, the participant is presented with a stimulus on a computer screen and responds on a keyboard. This translation process from the screen to a keyboard may engage working memory processes, with the indirect relationship between stimulus and response space constituting a form of symbolic transformation. When the demands on this transformation are minimized by aligning S-R space (i.e., responses are made directly at the stimulus locations), patients with cerebellar degeneration showed normal learning (Spencer & Ivry, 2009). In contrast, the same individuals exhibited no evidence of learning when the cues were indirect, although the responses were identical to those required with the direct cues. This dissociation argues against a direct cerebellar role in sequence learning.

The dichotomy between explicit and implicit processes has proved extremely useful for developing a taxonomic description of memory, as

well as identifying critical neural systems associated with different memory tasks. As noted earlier, the MTL appears to be essential for the formation of declarative memories. However, given that patients with lesions of this region do not have overt impairments of awareness, it remains a challenge to characterize the unique associative processes of this network. Models of MTL function have emphasized the importance of this system in the formation of contextual representations, associations that bind information across different sensory modalities or dimensions (Rudy & Sutherland, 1995; O'Reilly & Rudy, 2001). Keele and colleagues (Keele et al., 2003) extended this idea to the SRT task, arguing that the attenuation of SRT learning under dual-task conditions arises because the secondary task introduces noise into a cross-dimensional associative mechanism. Indeed, if the secondary stimuli are correlated with the SRT stimuli, learning is enhanced (Schmidtke & Heuer, 1997).

Error-Driven Learning: Insights from Studies of Visuomotor Adaptation

Another paradigm used to study motor learning centers on tasks in which the participant must adapt movements to overcome an experimentally induced perturbation. Here we focus mainly on tasks in which the mapping between visual and proprioceptive space is altered. Such perturbations can be achieved by introducing prismatic eyeglasses (fig. 3.2A) that impose a translational shift of the visual input (Redding & Wallace, 1988, 1993, 1997, 2005) or, with virtual reality systems, a visuomotor rotation (fig. 3.2B) in which the visual input is shifted in an angular manner (Cunningham, 1989; Imamizu & Shimojo, 1995; Krakauer, Pine, Ghilardi & Ghez, 2000). These types of perturbations are akin to using a computer mouse, but with a distortion of the mapping between the movement of the mouse and the movement of the cursor. In visuomotor adaptation experiments, rotations typically take on values ranging between 30° and 60°, with vision of the hand occluded to disguise the perturbation. In this chapter, we focus mainly on the findings from visuomotor adaptation tasks.

Visuomotor distortions may be overcome by recalibrating an internal model of the motor system. An internal model represents a mapping between a desired goal and the motor response necessary to achieve that goal. An error signal is used to recalibrate the mapping between desired goals and motor responses. This signal might be available online, allowing the person to make adjustments to the movement so as to achieve the desired location. Alternatively, the experimenter may only provide knowledge of results, ensuring that learning can only occur from trial to trial.

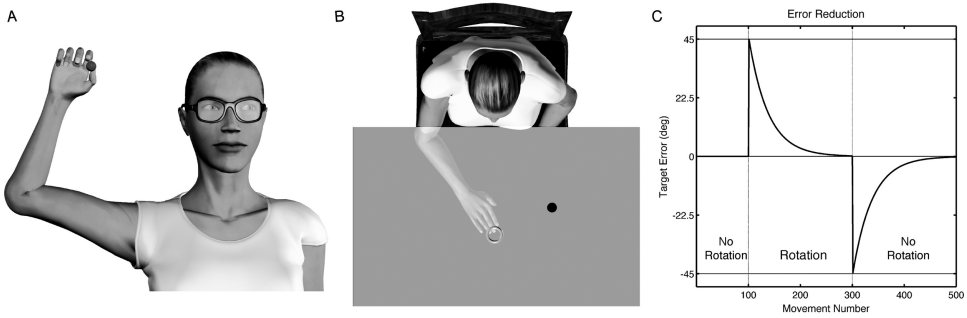

Figure 3.2
(A) Prism glasses induce a mismatch between eye-hand calibration, producing errors in throwing or reaching in the direction of the lateral prismatic shift. (B) Virtual reality environments are used to impose systematic transformation between actual and projected hand position. Vision of the limb is occluded. In this example, target was a green circle and a 45° rotation clockwise led to displacement of feedback location. (C) Hypothetical learning curve for a visuomotor rotation. A 45° rotation is presented for movements 100–300. Target errors are initially in the direction of the rotation, but with training, the person adapts. After learning, the rotation is removed (movements 301–500), and target errors are now in a direction opposite to the rotation (aftereffect).

Participants readily adapt to these visual perturbations, showing a reduction in target errors with training (fig. 3.2C). Learning to accommodate a visuomotor transformation could occur because of the implementation of an appropriate, volitional strategy—for example, consciously reaching in the opposite direction of the rotation. However, a pronounced aftereffect is observed when the rotation is removed and the original environment is reinstated: participants now produce an error opposite to the initial distortion. The presence of an aftereffect provides strong evidence that the motor system has truly been recalibrated.

In contrast to learning in the SRT task, a key feature in visuomotor adaptation is that it is error driven. Adaptation proceeds in a gradual manner, with the learning function typically conforming to an exponentially decaying function. This suggests that an error is used to continuously adjust the visuomotor mapping, with the magnitude of the change proportional to the error. Recent experiments have suggested that this trial-by-trial process of error reduction may occur over multiple timescales. There appears to be a temporally labile process of learning that learns quickly but with poor retention, as well as a slower process that exhibits better retention (Smith, Ghazizadeh & Shadmehr, 2006). It remains unclear

whether these processes reflect the operation of a single learning system with different time constants or instead the contributions of distinct neural systems.

An extensive literature points to a critical role of the cerebellum in error-based learning (Marr, 1969; Gilbert & Thach, 1977). Patients with cerebellar lesions have difficulty on a range of motor adaptation tasks (Rabe et al., 2009), including prism adaptation (Martin et al., 1996a), visuomotor adaptation (Tseng et al., 2007; Werner et al., 2009), and force field learning (Smith, 2005). Neuroimaging studies of visuomotor adaptation report activation changes in a broadly distributed network, including the cerebellum. In general, a reduction in cerebellar activity occurs over time, perhaps reflecting the reduction in error. However, one study (Imamizu et al., 2000) reported that this broad decrease in cerebellar activation was accompanied by a focal region showing an increase in activation during visuomotor learning, consistent with the development of a new internal model.

Activation increases are also observed in various cortical areas. During the initial stages of learning when error signals are large, activation increases are most prominent in frontal areas including dorsolateral PFC and anterior cingulate cortex (Jueptner et al., 1997; Shadmehr & Holcomb, 1997; Floyer-Lea & Matthews, 2004). Areas showing prominent changes over the latter part of training include premotor and motor cortex and posterior parietal cortex (Shadmehr & Holcomb, 1997; Sakai et al., 1998; Krakauer, 2003; Floyer-Lea & Matthews, 2004). Thus, with training, learning-related activation changes in the cortex shift from frontal areas to motor structures, a pattern consistent with the idea that learning may initially engage areas involved in goal selection and planning and then shift to areas involved in movement specification and execution. This shift in activation may reflect the automatization of the skill.

The activation of frontal areas during visuomotor adaptation suggests that explicit processes may be engaged, an assumption consistent with the observation that people are usually aware that the environment has been perturbed even if they cannot explicitly describe the change. Recall that a key component of visuomotor adaptation involves changes in motor execution. The sensorimotor system must be modified such that the action associated with a particular goal incorporates the effects of the altered environment. Thus, while explicit knowledge may not produce a benefit for motor execution, it is possible that explicit processes influence visuomotor adaptation.

As in SRT learning, a demanding secondary task can reduce performance gains during adaptation tasks (Taylor & Thoroughman, 2007, 2008; Galea,

Sami, Albert & Miall, 2010). The cost is not generic but maximal when the secondary-task stimuli occur simultaneously with movement errors (Taylor & Thoroughman, 2007). The effects of dual-task interference are not limited to conditions in which the participants are aware of the sensorimotor perturbation. Galea et al. (2010) reported similar reductions from a secondary task on the rate of visuomotor adaptation, regardless of whether the participants were aware or unaware of the manipulations. This suggests that implicit processes underlying adaptation entail some degree of overlap with those involved in secondary-task processing. Thus the interference may be unrelated to explicit processes used for adaptation. For example, the interference may result from an overload in sensory processing requirements for the primary and secondary tasks.

A different approach involves participants performing the two tasks in a sequential manner and observing whether they exhibit retrograde interference on the memory of the first task after performing the second (Ebbinghaus, 1885). Keisler and Shadmehr (2010) adopted this approach and found that a word-list learning task following motor adaptation selectively disrupted the most recent motor memories, while leaving older memories intact. This effect was not observed when the secondary task did not involve learning (i.e., vowel counting), suggesting that the point of overlap was within processes associated with learning per se. This direct involvement of explicit learning processes may reflect strategy development at a verbal level ("On the next trial, I will push to the left"). The effects of a verbal secondary learning task may disrupt the use of such strategies (Keisler & Shadmehr, 2010).

Finally, a more direct approach for comparing implicit and explicit processes in visuomotor adaptation is to manipulate the manner in which the environmental perturbation is introduced. In the standard paradigm, a rotation is introduced in a single step: the participant is performing a reaching task, and a large rotation is abruptly imposed. With the abrupt introduction of the rotation, a large error occurs between the cursor and hand, a change that participants are generally aware of. An alternative approach is to introduce the rotation in a gradual manner. For example, the rotation may be increased by a few degrees every few trials (e.g., Kagerer, Contreras-Vidal & Stelmach, 1997). In the gradual condition, the added error with each increment falls within the bounds of motor noise, and adaptation occurs without awareness.

Performance is generally more variable when the rotation is introduced abruptly compared to when it is imposed gradually. This variability may reflect the contribution of explicit processes. Some participants may opt

to test strategies when they experience the large error following the onset of the rotation; other participants may simply rely on implicit processes (Martin et al., 1996b). Strategic processes have also been proposed to account for individual differences in adaptation rates. Participants with higher spatial working memory capacity show faster adaptation, presumably because they are able to use their mental rotation abilities to compensate for the rotation (Anguera, Reuter-Lorenz, Willingham & Seidler, 2009). Moreover, while older adults learn at a slower rate compared to younger individuals (Fernández-Ruiz, Hall, Vergara & Dıíaz, 2000; Bock, 2005), this difference is attenuated for older adults who are able to explicitly describe the perturbation (Heuer & Hegele, 2008). Moreover, older adults, despite having slower adaptation rates, show comparable and even larger aftereffects (Fernández-Ruiz et al., 2000; Bock, 2005; Heuer & Hegele, 2008). Thus explicit knowledge may provide a means to bootstrap adaptation, allowing for the generation of a strategy to facilitate learning, even if such a strategy does not directly impact implicit learning within the motor system.

Mazzoni and Krakauer (2006) devised a clever way to examine the interaction of explicit and implicit processes in visuomotor adaptation. Participants were presented with a display of eight visual landmarks, spaced 45° apart (fig. 3.3A). In each trial, a visual target appeared at one of the landmarks. After a series of reaches, a 45° counterclockwise rotation was introduced. The participants were then informed about the 45° counterclockwise rotation and instructed to counteract it by aiming 45° in the clockwise direction, using the neighboring landmark as an aiming target (fig. 3.3A). The implementation of a strategy resulted in good performance and the immediate cancellation of the visual error (fig. 3.3B). However, as training continued, participants spontaneously increased the angle of their aim, reaching to positions more than 45° in the clockwise direction (fig. 3.3B). That is, their performance became worse with practice!

To account for this effect, Mazzoni and Krakauer (2006) argued that implicit processes for visuomotor adaptation operate on an error signal representing the difference between the aiming location (predicted end point) and the feedback location. Although the participants choose to aim 45° clockwise from the target (to offset the rotation), the motor system receives an error, since a substantial difference exists between the aiming location and the feedback location. To reduce this error, the aiming location is shifted in the clockwise direction. What is striking here is that the operation of this implicit adaptive process results in an increase in error as defined by the target location. Indeed, the participants were puzzled to watch their performance deteriorate as training progressed. This result

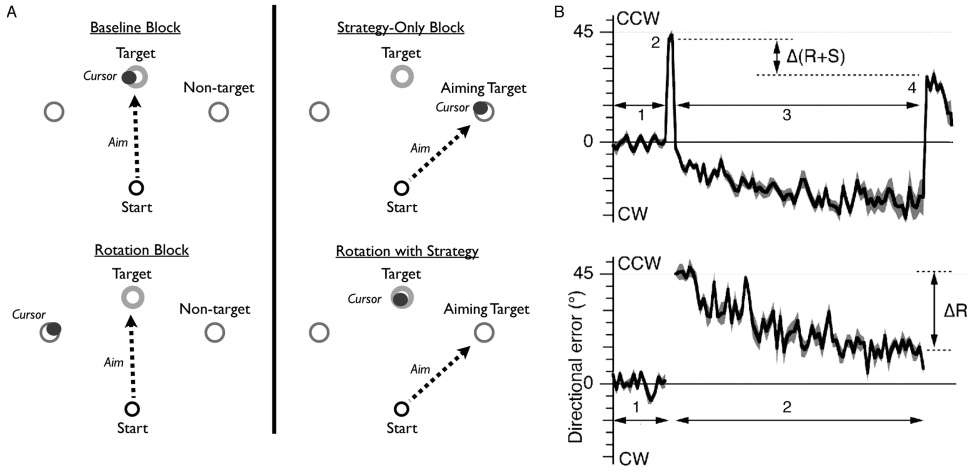

Figure 3.3

(A) In the baseline block, participants move a cursor, representing hand position, toward a cued target (thick circle), which could appear at one of eight locations. In the strategy-only block, participants are trained to reach to an aiming landmark (thin circle), 45° clockwise to the target. For the two rotation probes, feedback of hand position was rotated 45° in the counterclockwise direction. In the rotation with strategy block, participants were instructed to move to the aiming landmark to compensate for the rotation. (B) Rotation with strategy: Target errors are centered around zero during the baseline block (1). Large errors are observed when the rotation is unexpectedly introduced (2). When instructed to use the strategy, movements are initially very accurate, but over time, performance deteriorates, with error drifting in the direction of the strategy (3). Aftereffect is observed when participants are instructed to stop using strategy (4). Adapted from figure 2 from Mazzoni, P. & Krakauer, J. W. (2006). An implicit plan overrides an explicit strategy during visuomotor adaptation. *Journal of Neuroscience*, *26*(14), 3642–3645, reprinted with permission.

points to a strong segregation of explicit and implicit processes. The implicit system does not have access to the strategy; rather, the mechanism underlying implicit learning assumes that the aiming location should coincide with the feedback location and uses this error to update an internal model.

A similar effect has been reported in a drawing experiment in which gain was adjusted so that visual feedback of a movement was either greater or lesser than the actual distance of the hand movement (Sülzenbrück & Heuer, 2009). The participants were provided with an inappropriate strategy, one that called for compensation to a larger gain shift than was actually introduced. While participants initially adopted the instructed strategy—and

thus increased the end point error—the motor system eventually adapted to the appropriate gain. This study further supports the segregation between implicit and explicit adaptive processes.

Studies in which participants are given a strategy to compensate for a visuomotor perturbation place explicit and implicit processes in opposition with each other. The strategy provides participants with a guide concerning where to aim their movement, influencing the planning stage of the movement. In contrast, the implicit system operates on the execution stage, realigning the sensorimotor system so that the arm moves toward the desired location. In SRT studies, instructions, when given, are also directed at the selection stage: the participant is informed of the embedded sequence. However, in SRT learning, such manipulations supplement implicit learning in that both explicit and implicit systems are designed to learn the same information, the sequence of stimuli and responses. A strong test of the degree of independence between implicit and explicit processes in SRT learning would require developing an experimental manipulation in which the two systems are put in opposition with each other.

Representation of Learning as Probed through Transfer and Generalization

Transfer studies have been used to explore the representational changes that occur during skill acquisition. In the typical transfer study, participants are trained with one set of effectors and then tested with a different set. Aspects of skill that show strong transfer are taken to indicate components that are represented at an abstract or task level. Aspects of skills that show weak transfer are taken to indicate components that are represented at an effector or response level (Imamizu & Shimojo, 1995). In sequence learning, near-perfect transfer has been observed when the task is initially performed with finger responses and transfer is tested with arm movements (Cohen, Ivry & Keele, 1990), indicating that sequence learning is effector independent. Perfect transfer suggests that learning is of the sequence of stimuli or the sequence of stimulus-to-response mappings. Alternatively, the response code may be represented as a spatial map of locations or goals.

Transfer is not always perfect. Studies show a slight reduction in measures of learning for transfer between manual and vocal responses (Keele et al., 1995). Moreover, with extended practice, the degree of transfer in sequence learning is substantially reduced (Karni et al., 1998). A skilled pianist may be able to use her left hand to play the right-hand notes of a

learned piece, but performance will not be as fluid or facile. With consolidation, skill representation likely involves some degree of learning at the response level (Grafton et al., 1998).

Researchers have also used transferlike manipulations to examine the reference frame of a learned representation. In one SRT study, participants learned a sequence and were asked to move to a new seat such that the left side of the keyboard was now on the right side. Training resumed in the new arrangement, with the sequence either following the same pattern as before or following a mirror-reversed pattern. Performance was best when the sequence was reversed, indicating that learning was in an egocentric frame of reference (relative to body) rather than in an allocentric frame of reference (relative to the world) (Witt, Ashe & Willingham, 2008; see also Liu et al., 2007).

What remains unclear from this study is whether the learned representation is effector centered. For example, if the index finger was used to start the sequence, reversing the sequence (and participant) would mean that the sequence would again start with the index finger. To address this issue, Witt et al. (2008) had participants initially learn the sequence with their hand in a supine configuration (palm face up). During transfer, the posture was altered such that the hand was now in a prone configuration (palm face down). The participants showed a high degree of transfer, indicating that the sequence was represented in an egocentric reference frame centered on the head or body, rather than a frame based on the effector (e.g., the hand). As in the earlier transfer studies, these results indicate that a large component of learning is not linked to specific muscles or movements but is situated in a space relative to the body. It should be noted that the effects of awareness in these studies are unclear. It may be that the reference frames underlying explicit versus implicit learning processes are different.

Transfer and generalization studies have been used to ask similar questions regarding sensorimotor adaptation. Learning here can occur in a coordinate system that is in extrinsic space and centered on the hand (Vindras and Viviani, 1998). When participants are trained to learn a visuomotor rotation at a specific location (e.g., target in upper-right quadrant), the degree of generalization to other locations drops off sharply as the angular distance between the training and test locations increases (Krakauer et al., 2000). However, a small yet significant degree of transfer extends across the entire workspace. Moreover, specific components of adaptation transfer across hands, and these effects occur in extrinsic space. That is, training with the right hand to a rotation in the upper-right

quadrant is associated with the largest left-hand transfer in the same quadrant (Imamizu & Shimojo, 1995; Sainburg & Wang, 2002). Thus the learned representation exhibits some degree of abstraction, both in terms of generalization to untrained locations and across effectors. In this manner, implicit learning for visuomotor adaptation and sequence learning are similar, despite the underlying task and computational differences.

The picture becomes more complicated when considering generalization effects following adaptation in a novel force field (Shadmehr & Mussa-Ivaldi, 1994). Initially the movements are perturbed in the direction of the force. With practice, participants learn to counteract the forces so as to move straight to the target. When the force field is unexpectedly removed, an aftereffect is observed, with the movement now shifted in the opposite direction. Thus participants have learned the dynamics of the force field, rather than adopting a strategy that generically minimizes the perturbing effects of the forces (e.g., stiffening the limb). When participants train in a particular workspace, generalization is greatest to positions in the workspace where the mapping between joint orientation and the pattern of forces is similar to the training workspace (Shadmehr & Mussa-Ivaldi, 1994).

For the present discussion, two important points stand out. First, participants modified their motor output to produce straight trajectories. This suggests that optimization at the planning level outweighs costs related to execution factors such as torque or energetic expenditure, assuming that these are higher when producing movements that oppose the force field (Thoroughman, Wang & Tomov, 2007; Kistemaker, Wong & Gribble, 2010). The system appears to emphasize modifying movements to maintain a fixed goal or plan rather than modifying the plan itself. Second, the pattern of generalization indicates that learning occurs in intrinsic, joint-centered coordinates (Shadmehr & Mussa-Ivaldi, 1994; Thoroughman & Shadmehr, 2000; Donchin, Francis & Shadmehr, 2003). This pattern of generalization further supports the notion that implicit learning is occurring at the level of motor execution rather than movement planning.

Intermanual transfer designs have also been employed in studies of force field learning. Adaptation from training with one arm transfers to the other arm (Criscimagna-Hemminger, Donchin, Gazzaniga & Shadmehr, 2003). The pattern of transfer is in extrinsic space, such that if one arm learns a clockwise force field, performance with the other arm is better if the force field is unchanged, compared to when it is reversed. This pattern of transfer, however, must be qualified. Force field learning appears to be asymmetric: transfer is observed from the dominant to the nondominant arm, but not in the reverse direction (Criscimagna-Hemminger et al., 2003).

Moreover, Malfait and Ostry (2004) suggest that intermanual transfer following force field learning may be limited to conditions in which participants are aware of the perturbation. They failed to observe transfer from the right to left arm when the force field was introduced in small, gradual steps. This null result is especially surprising given that this form of learning is frequently considered the paradigmatic example of implicit motor learning. It may be that intermanual transfer involves rather generic information—for example, that an opposing force should be generated in the clockwise direction—rather than the true adaptation of an internal model. Or it may be that awareness puts the system in a mode that enables abstract-level learning, even if the acquired representations are implicit.

The Interaction and Integration of Explicit and Implicit Processes

In terms of our distinction between planning and execution, we might expect that strategic effects operate at the level of goal selection and response planning. This point is made clear when considering the Mazzoni and Krakauer (2006) study. As noted earlier, participants were instructed to move to an aiming location next to the target in the clockwise direction, an instruction designed to influence the planning level. This strategy produced an immediate benefit in performance but also increased the error used by the implicit learning mechanisms. Indeed, the conflict between explicit and implicit processes is confounded with manipulations that influence planning and execution levels of performance.

We further explored this issue in a recent study (Taylor & Ivry, 2011). If the implicit adaptation system fully overrides the explicit system, one would expect performance to continue to deteriorate until the error reached 45°. This seemed highly unlikely; at some point, we expect participants would make some sort of adjustment. Indeed, when the duration of training was extended, the size of the error peaked at around 25° and then reversed until performance was nearly perfect. To account for this nonmonotonic behavior, we developed a novel state space model in which performance is the result of two processes, each modified by its unique error term (fig. 3.4A). First, the difference between the aiming location and feedback location defines an aiming error, a signal that is used by the implicit system to recalibrate an internal model. Second, the difference between the target and feedback location defines a target error, a signal that is used to adjust the strategy.

Our simulations show that when these two learning mechanisms operate in parallel, one observes an initial drift away from the target, with

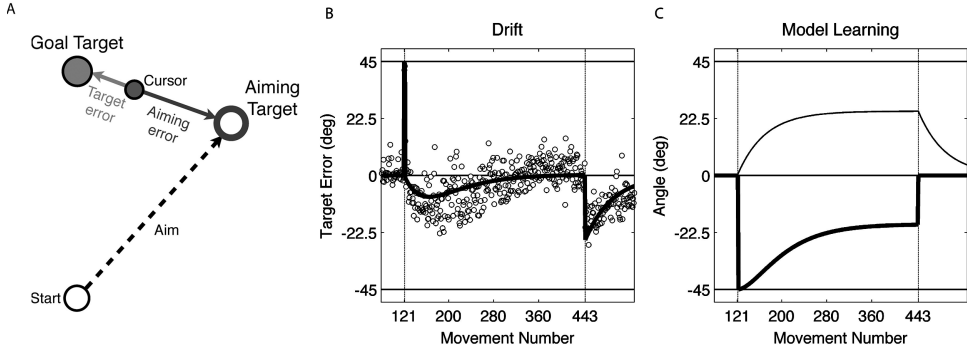

Figure 3.4

(A) Implicit adaptation is based on aiming error, the difference between the aiming location and feedback. Strategy adjustment is based on target error, the difference between the target location and feedback. (B) When strategy is implemented after onset of rotation, target error is small (performance is accurate), but aiming error is large, and implicit adaptation produces deterioration in accuracy. As target error becomes large, the effect of strategy adjustment becomes more prominent, leading to a reversal of the drift. System eventually stabilizes although the two learning processes continue to operate. Aftereffect evident when the rotation is removed reveals magnitude of implicit adaptation. Circles: observed data for one participant. Black: model fit. (C) Dynamics of learning within the implicit system (visuomotor adaptation, thin) and strategy (thick) following trial-by-trial updates with the two error signals.

eventual correction (fig. 3.4B). Importantly, the model posits that the two processes are always functional. Drift is prominent during the early stages of strategy implementation because aiming error is large and target error is small; thus changes in performance are dominated by learning within the implicit system. However, as target error becomes large, strategy changes become more prominent (fig. 3.4C). Even when performance stabilizes with minimal error, the two processes continue to operate, creating a stable tension (fig. 3.4C). Consistent with this hypothesis, the model accounts for the fact that the aftereffect observed when the rotation is turned off is larger than the maximum drift (Taylor & Ivry, 2011).

This modeling enterprise raises an interesting question: why is drift not observed in standard visuomotor rotation experiments given that participants, at least under some conditions, spontaneously develop a strategy? An important methodological difference between the task used by Mazzoni and Krakauer (2006) and the standard task is the presence of landmarks. In Mazzoni and Krakauer's task, landmarks were present every 45° to provide a reference point for the aiming strategy. In the standard task,

these landmarks are absent; participants only see a stimulus at the target location. We propose that the landmarks serve as a proxy for the predicted location of a movement. When these landmarks are absent, the participant's sense of 45° is likely uncertain, and thus the weight given to the aiming error term is attenuated. We tested this idea by comparing conditions in which the landmarks were always present, disappeared at movement initiation, or were never presented. Consistent with the certainty hypothesis, the degree of drift was attenuated as uncertainty increased (Taylor & Ivry, 2011). In fact, when the landmarks were never present, drift was minimal throughout the training block. These results are similar to the "target-pointing effect" on adaptation, where adaptation scales with the degree of visual error information available to the motor system (Welch & Abel, 1970).

Our modeling efforts provide a first exploration of the interaction of strategic and implicit processes. Consistent with the conjecture of Mazzoni and Krakauer (2006), it appears that the implicit system is completely isolated from the strategy and is involved only in improving movement execution. In contrast, the strategy is adjusted with an error signal that reflects the movement goal, minimizing target errors. Learning within this system modifies a representation relevant for planning, ensuring that the outcome of the action achieves the desired goal.

This synergistic, two-process interpretation may also provide a different perspective for understanding the consequences of neural pathology on specific learning processes. Consider the effects of cerebellar damage on sensorimotor control and adaptation. One might consider the impaired performance reflective of the operation of a compromised system, one that is functioning at a suboptimal level. Alternatively, the patients' performance may reflect a compensatory process, one in which they have come to rely on alternative forms of control. Lang and Bastian (2002) observed that patients with cerebellar damage performed surprisingly well when asked to make rapid, complex drawing movements, reaching a performance level comparable to that of control participants. However, when patients were required to perform a concurrent secondary task, their drawing performance was markedly reduced (Lang & Bastian, 2002). These results suggest that the patients may have relied on a strategy-based system, one that was taxed by the inclusion of the secondary task.

We tested this idea by instructing patients with cerebellar degeneration to use an explicit strategy to compensate for a visuomotor rotation. The patients were capable of using the strategy to offset a visuomotor rotation. More importantly, they showed minimal maladaptive drift over the course

of training (Taylor, Klemfuss & Ivry, 2010), consistent with the idea that the implicit adaptation system was impaired.

However, these results fail to explain why patients do not generate their own compensatory strategies. For example, in visuomotor adaptation studies, some patients will continue to produce large and consistent errors for over a hundred trials. To understand this paradoxical behavior, it is useful to consider that while an explicit strategy does not influence implicit adaptation, the converse may not be true: implicit processes may inform explicit strategies. Typically, visual errors in rotation studies are quite large (Weiner, Hallett & Funkenstein, 1983), and the patients are aware of their poor performance. However, given the complex rotational pattern of the errors, generating a successful strategy may not be entirely obvious. The error pattern would place a high demand on the attention and working memory areas required to develop the appropriate strategy.

Patients with PFC lesions have been tested to explore the importance of working memory and cognitive control processes on motor learning tasks. Disruption of PFC with TMS has been shown to selectively disrupt SRT learning (Pascual-Leone et al., 1996). More importantly, patients with PFC lesions also exhibit pronounced deficits in visuomotor adaptation (Slachevsky et al., 2001, 2003; Ivry et al., 2008), a result that challenges the notion that learning is limited to processes typically associated with implicit learning. These patients have difficulty describing the perturbation or, when aware of it, have difficulty reporting what action would be required to compensate for the perturbation (Slachevsky et al., 2001, 2003). Thus their deficit may in part be related to difficulty with generating strategies for motor adaptation.

Conclusion

The terms “explicit” and “implicit” have proved useful for describing subjective states but have also presented problems when employed as theoretical constructs. Our emphasis here has been to consider how processes associated with explicit and implicit learning may differ, and what the computational implications of these differences are for theories of motor learning. Explicit processes may best be related to the desired goals of an action. Returning to our initial billiards example, representations that are accessible to awareness are related to selecting which ball is to be pocketed and how the cue ball will be approached to achieve this goal. On the other hand, implicit processes figure prominently in establishing the fine calibration and coordination required to execute the desired movement, defining

the parameters necessary to execute the movement. Both the selected movement and the execution of that movement may result in performance errors that are used to refine future movements. Our modeling work on visuomotor adaptation makes transparent the fact that explicit and implicit processes can operate on very different error signals. Strategic planning processes are sensitive to performance errors. In contrast, motor execution processes are sensitive to prediction errors between a desired and actual outcome. Strategic planning processes help define what the desired movement should be, while execution processes are essential for the successful implementation of the desired movement. These processes work synergistically to produce skilled actions.

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4 Cognitive Foundations of Action Planning and Control

David A. Rosenbaum

Introduction

This chapter is concerned with the cognitive foundations of the planning and control of physical actions. The field to which it belongs, apart from cognitive psychology or cognitive neuroscience, is called motor control. Though the term "motor control" traditionally suggests a division between acting and perceiving, the study of motor control is meant to contribute to the understanding of action more generally.

Researchers in motor control address four core problems: (1) the perceptual-motor integration problem; (2) the serial order problem; (3) the degrees-of-freedom problem; and (4) the learning problem. The perceptual-motor integration problem relates to the fact that actions have perceptual consequences. The question is how actions are chosen that yield desired perceptual consequences. The serial order problem relates to the fact that successive behaviors must be appropriately sequenced and timed. The question is how such sequencing and timing are achieved. The degrees-of-freedom problem relates to the fact that for any given task there are usually an infinite number of possible solutions. The question is which solutions are chosen and by what means. The learning problem relates to the fact that performance typically benefits from experience. The question is how such changes come about.

This chapter summarizes some of the research that bears on each of these problems. Space does not permit a full treatment. More can be learned by consulting other sources such as journals where these problems are routinely considered, including *Journal of Experimental Psychology: Human Perception and Performance*, *Experimental Brain Research*, *Human Movement Science*, *Nature Neuroscience*, *Journal of Motor Behavior*, and *Motor Control*. Several books have been devoted to these topics. To name just a few, Schmidt and Lee (2005) provided a rich source of information about

motor skill learning; Shadmehr and Wise (2005) pursued a neurocomputational approach; Kandel, Schwartz, and Jessell (2006) and Gazzaniga (2009) provided in-depth treatments of the neural basis of motor control; and I wrote a book about motor control which mainly pursues a cognitive psychological approach (Rosenbaum, 2010).

The Perceptual-Motor Integration Problem

When you carry out physical actions, you receive sensory feedback. The feedback helps you make corrections. The corrections are possible only because you have some idea (typically unconscious) of what perceptual outcome you want. The corrections, too, are rarely made with awareness.

Two thinkers can be said to have set the agenda for research on the perceptual-motor integration problem: James Clerk Maxwell (1831–1879), the great Scottish physicist; and Hermann von Helmholtz (1821–1894), the great German physiologist.

Maxwell and Feedback Control

James Clerk Maxwell is rarely mentioned in connection with perceptual-motor integration. In fact, mentioning him here may come as a surprise to some readers. This is because Maxwell is best known for his equations ("Maxwell's equations") which established that electricity, magnetism, and light all occupy the same electromagnetic spectrum. Albert Einstein called this idea the second great unification of physics, the first one being, according to Einstein, Isaac Newton's three laws of motion. Maxwell's recognition that electricity, magnetism, and light are actually one and the same may be viewed as a precursor to the idea that perception and action share a common code (Prinz, 1990). The common-code idea can be said to have drawn inspiration from the penchant for parsimony that Maxwell's equations exemplify.

Maxwell was also the first to lay out, in mathematical terms, the core ideas of feedback control theory, doing so in his paper "On Governors" (1867–1868), where he addressed the problem of controlling steam engines. Since Maxwell's introduction of a mathematically expressed feedback control theory, engineers have expanded and refined it, permitting sophisticated feedback-based control in virtually all the technology used today. Scientists concerned with human and animal perceptual-motor integration have also applied concepts of feedback control theory to investigate how its concepts apply to such phenomena as the regulation of pupil diameter (Stark, 1968), the control of aiming (e.g., Elliott, Helsen & Chua, 2001), and adaptation to distorted visual feedback (e.g., Mazonni & Krakauer,

2006). A book about feedback control theory for experimental psychologists was written by Jagacinski and Flach (2003). A book that suggested ways in which feedback might be used at different levels of control, *Plans and the Structure of Behavior*, by Miller, Galanter, and Pribram (1960), is often credited with being a cornerstone volume in the emergence of cognitive science.

Helmholtz and Feedforward Control

The other major thinker who set the agenda for research on perceptual-motor integration was Hermann von Helmholtz. He suggested that perception entails unconscious inference, a hypothesis he reached by considering a variety of perceptual phenomena, such as visual illusions and perceptual consequences of voluntary movements. In one demonstration, Helmholtz pressed gently with his finger against the lid of his own open eye, keeping his other eye shut. When he did so while trying to maintain visual fixation on a single point in the external environment, he noticed that the visual world seemed to bounce back and forth. When he removed his finger and simply let his eye sweep back and forth across the same visual scene, the world appeared stationary.

Helmholtz wondered what accounted for the contrasting visual perceptions associated with pushing on his eye with his finger versus moving his eye back and forth in the normal fashion. His answer was that when normal motor commands are used to generate saccades, an unconscious expectation is formed for the associated retinal changes. By contrast, when the eye is pushed with the finger, no retinal change is expected, and the shift of the visual world across the retina is ascribed to external motion rather than to internal motion.

Through this simple demonstration, then, Helmholtz inferred unconscious inferential processes. In so doing, he set the agenda for much of modern cognitive neuroscience. The computational approach that is now taken for granted in cognitive neuroscience was inspired by Helmholtz. Via his work on unconscious inference, Helmholtz can be said to have provided the first evidence for feedforward control (anticipation of perceptual consequences of forthcoming movements). The feedforward concept has been brought to the fore in more modern times by such authors as Duhamel, Colby, and Goldberg (1992), Sperry (1950), von Holst and Mittelstaedt (1950), and Wolpert and Flanagan (2001).

Bimanual Interactions

My mention of Maxwell and Helmholtz is not meant to set these two intellectual giants at loggerheads. In fact, though there was much debate in the 1960s about whether feedback is really necessary for successful

motor control (Keele, 1968), it is now generally accepted that feedback and feedforward are both important.

This rapprochement can be illustrated by briefly reviewing two studies that were concerned with a dramatic and easily demonstrated phenomenon in human motor control: two-hand interference. If you try to draw a circle with one hand while drawing a square with the other hand, neither shape is likely to be as close to its ideal form as when it is drawn on its own. Much research has been done to uncover the source of such effects. For a recent review, see Oliveira and Ivry (2008).

One study of bimanual interactions, by Mechsner, Kerzel, Knoblich, and Prinz (2001), showed that the difficulty of drawing two shapes at the same time stems from perceptual limitations. Mechsner et al. asked participants to turn two cranks beneath a tabletop (fig. 4.1). The cranks were out of view, but two flags, one associated with each crank, were visible above the table surface. The flags were attached to the cranks via gears that affected the phase relation of the flags. In some conditions, the gears caused the flags to turn with a simple phase relation even though the cranks were turned with a complex phase relation. In this situation, the cranking became much easier than when the two flags directly reflected the turning of the cranks. Mechsner et al. concluded that the simplified perceptual representation permitted two-hand movement patterns that were very difficult otherwise. These authors therefore capitalized on feedforward control to elucidate the locus of bimanual interactions.

Another study that capitalized on feedback control to do the same, and led to the same main conclusion, was conducted by Rosenbaum, Dawson, and Challis (2006). We had participants engage in a task we called "haptic tracking." We asked participants to keep their hands in contact with two moving objects (fig. 4.1). The participants had to maintain light touch on the objects, which were two disks that moved either in square patterns or in circular patterns. When the disks moved in circular patterns, the disks moved at different frequencies in some conditions, causing the phase relation between the disks to vary continuously. People cannot generate squares and circles at the same time, nor can they produce two circles at the same time with different frequency ratios and with continuously varying phase relations. Nevertheless the participants in our haptic tracking experiments could perform all the tasks virtually perfectly with virtually no practice. This outcome suggests that when the intentional system that normally drives bimanual performance is bypassed, limits to bimanual performance can disappear. Having a difficult feedforward problem impedes performance, as Mechsner et al. argued. But when haptic feedback can be

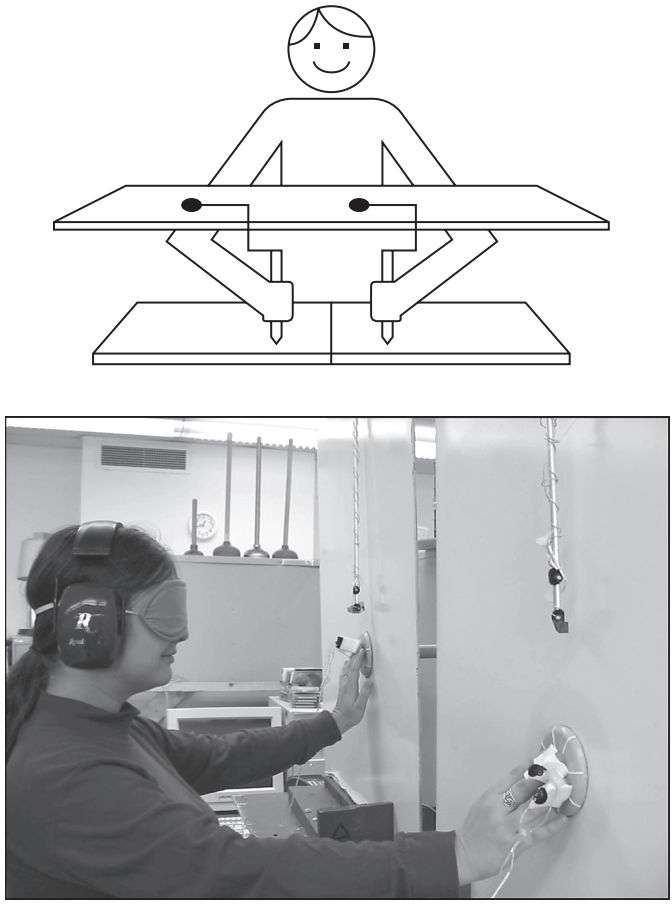

Figure 4.1
Two procedures used to study bimanual interactions. *Top row*: A participant turning cranks to see two rotating flags. Reprinted with permission from Macmillan Publishers Ltd. (*Nature*): Mechsner, F., Kerzel, D., Knoblich, G. & Prinz, W. (2001). Perceptual basis of bimanual coordination. *Nature*, *414*, 69–73). *Bottom row*: A participant lightly touching two moving disks. (From Rosenbaum, D. A., Dawson, A. M. & Challis, J. H. [2006]. Haptic tracking permits bimanual independence. *Journal of Experimental Psychology: Human Perception and Performance*, *32*, 1266–1275. Reprinted with permission from APA.)

used to simplify the control problem, the task gets much easier, again in accord with the conclusion of Mechsner et al.

The Serial Order Problem

The second problem in the study of motor control is the serial order problem. As mentioned earlier, at issue here is understanding how successive behaviors are appropriately sequenced and timed.

Just as two major thinkers established core ideas for consideration of the perceptual-motor integration problem, two major thinkers created the pillars for research on the serial order problem: the British physiologist Charles Sherrington (1857–1952) and the American physiologist Karl Lashley (1890–1958).

Sherrington conducted groundbreaking research on reflexes, for which he was awarded the Nobel Prize in Physiology or Medicine. Based on his work, Sherrington (1906/1947) argued that reflexes comprise the basis for all physical actions. According to this view, every physical action can be viewed as a direct response to some immediately preceding stimulus, a major component of which is feedback from the physical action completed just before. This concept laid the groundwork for behaviorism, whose foothold was particularly strong in America.

Karl Lashley, in a chapter published in 1951, challenged the reflex-based view of action. He argued that behavioral sequences do not unfold in such a way that each response is triggered by feedback from the immediately preceding response. Rather, he argued, entire series of forthcoming acts are prepared in advance of their execution. In support of this hypothesis, Lashley noted that interruption of sensory pathways does not necessarily disrupt behavioral sequencing, contrary to any simpleminded S-R chaining hypothesis. He noted as well that many responses occur too soon after preceding stimuli that might be thought to trigger them. The example he gave for such rapid responding was a pianist making successive keystrokes with interresponse times that were too short to be ascribed to known feedback delays.

By saying that sequences of movements are planned in advance, Lashley theorized that there are memory representations geared to the future. As a case in point, he relied on language production, drawing attention to errors in speech that imply preparation of upcoming utterances. An example one can cite is “You hissed all my mystery lectures” rather than the otherwise intended “You missed all my history lectures.” Errors like this, attributed to the warden of New College (Oxford), William Archibald

Spooner (1844–1930), and so referred to as spoonerisms, indicate that the speaker has mentally prepared what he or she is going to say before saying it.

Creating and Implementing Plans

Although Lashley pointed out that plans establish mental structures for forthcoming actions, he and others who made similar claims (see Fromkin, 1970) had little to say about how those plans are assembled or executed in real time. Hoping to shed light on this issue, Albrecht Inhoff, Andrew Gordon, and I studied the time people took to choose between pairs of response sequences that were specified in advance (Rosenbaum, Inhoff & Gordon, 1984). In our studies, we asked college students to associate one extended keyboard sequence with one visual stimulus (the letter *x*) and to associate another extended keyboard sequence with another visual stimulus (the letter *o*). When the *x* or *o* appeared on a computer screen, the subjects were supposed to produce the associated sequence as quickly as possible. The idea behind the study was that if Lashley was correct that entire sequences of responses are represented in advance, then times to decide between the sequences should reflect the properties of the sequences as a whole, not just the two alternative first responses.

In one of our studies, we asked participants to choose between pairs of keyboard sequences involving the left index finger (i), the left middle finger (m), the left ring finger (r), the right index finger (I), the right middle finger (M), and the right ring finger (R). The choices varied in length: (1) i versus I, (2) ir versus IR, and (3) irm versus IRM. We found that the choice reaction time for the first response increased with the number of keypresses in the forthcoming sequence. Thus the time to make the same keypress (either i or I) in response to the same stimulus (*x* or *o*) got longer as more responses followed. Similar results were obtained in simple RT tasks, where there was no choice between sequences. When participants knew which sequence had to be performed, the time to start the sequence likewise increased with its length (Sternberg, Monsell, Knoll & Wright, 1978).

A model that accounts for both sets of results relies on the idea that plans for forthcoming behaviors are hierarchically organized and the plans are successively "unpacked" in a way that directly depends on their hierarchical structure. The model predicted not only that sequence initiation times would increase with sequence length but also that interresponse times would, as well. This prediction was confirmed in the studies mentioned earlier and in other studies of rapid keyboard performance (Collard & Povel, 1982; MacKay, 1987; Rosenbaum, Kenny & Derr, 1983; Verwey,

2001). The same prediction was also confirmed in studies of *verbal* recall: times between successively recalled verbal items were also found to grow with the sequence length (Reitman & Rueter, 1980). The qualitative similarity of the response time patterns in the verbal tasks and in the motor tasks suggests that behavior was controlled in the same way in both contexts.

Building on What Has Been Established

In the experiments described above, participants chose between sequences that differed from start to finish. However, in the sequence-choice procedure generally, the choices do not have to be between two entirely different sequences. They can share elements at the beginning, at the end, or in between. This fact was exploited in other experiments (Rosenbaum, Hindorff & Munro, 1987), where it was found that for two sequences of fixed length, the later the first uncertain response, the shorter the choice RT.

It was possible to explain this result by adding a further assumption to the hierarchical unpacking model outlined above. According to the added assumption, participants took advantage of what was established regarding the alternative sequences, creating a complete plan up to the first point of uncertainty prior to identifying the choice signal and then completing the plan after the choice signal was identified (Rosenbaum, 1987).

Another way the motor planning system can take advantage of what has been established is to exploit similarities between forthcoming responses and recent responses. Performance of a given behavior should be affected by its relation to the previous behavior if there is a memory for the previous behavior. If such a memory exists and if it can be drawn on to produce upcoming sequences, an upcoming sequence should be easier to produce if it matches the last behavior than if it does not.

A phenomenon that illustrates the benefit of sequence repetition is one I happened on while playing the violin in a community orchestra (fig. 4.2). Amateur musicians were asked to play a passage in which a quarter note was followed by two eighth notes, repeated over and over again. At first, we were asked to play the passage in a way we could easily manage: down bow for the quarter note followed by two up bows for the eighth notes. Then we were asked to play the passage in a way we found much harder: alternating down and up bows. We "fell apart" while trying to play the passage this second way. I wondered why we found it so difficult.

Normally, when the durations of successive notes are the same, alternating between down and up bows is very easy. I was led to the hypothesis that the source of the problem was that the mapping of bow directions to

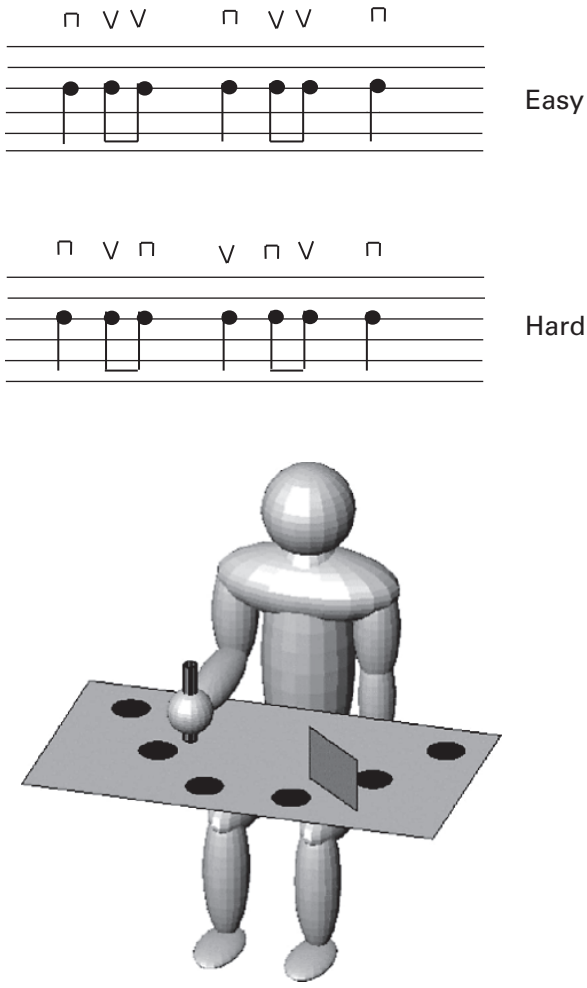

Figure 4.2
Two contexts in which the parameter remapping effect is observed. *Top row*: Bowing when the mappings of bow directions are constant (easy) or changing (hard) (from Rosenbaum et al., 1986). *Bottom row*: Moving a handheld dowel between flat circular targets on a table with an obstacle standing between two of the targets. (From Van Der Wel, P. R., Fleckenstein, R., Jax, S. A. & Rosenbaum, D. A. [2007]. Hand path priming in manual obstacle avoidance: Evidence for abstract spatio-temporal forms in human motor control. *Journal of Experimental Psychology: Human Perception and Performance*, *33*, 1117–1126. Reprinted with permission from APA.)

bow durations kept changing in the second version, whereas it remained the same in the first. Such an explanation rested on the idea that mappings between movement parameters—directions and durations, in this case—are preserved in memory. If the mappings change, those changes take time to implement, and the remapping process may be error prone.

My colleagues and I tested this hypothesis in experiments where college students engaged in a somewhat different task: reciting the first *n* letters of the alphabet over and over again as quickly as possible with the requirement that they always alternate between stressed and unstressed pronunciations (Rosenbaum, Weber, Hazelett & Hindorff, 1986). When *n* was even, the mappings of stresses to letters remained fixed in successive productions, but when *n* was odd, the mappings of stresses to letters switched in successive productions. Participants had a much harder time reciting the first *n* letters of the alphabet when *n* was odd than when *n* was even; this difficulty grew as *n* decreased. The hardest condition of all was $n = 3$, which was the one for which the rate of hypothesized parameter remapping was the highest.

My coauthors and I called the slowing of performance when parameter mappings change the *parameter remapping* effect. We found that the effect applied not only to violin bowing and to speaking but also to the production of keyboard sequences. When a given finger pressed a key the same number of times in successive production cycles, the cycles could be generated more quickly than if the same finger pressed its key different numbers of times in successive production cycles (Rosenbaum et al., 1986). Obtaining evidence for the parameter remapping effect across a range of tasks—in violin bowing, in speaking, and in keyboarding—provided evidence for the generality of the underlying process.

Similar sorts of sequential effects have emerged in other studies. One example is the handpath priming effect (Griffiths & Tipper, 2009; Jax & Rosenbaum, 2007, 2009; Van Der Wel, Fleckenstein, Jax & Rosenbaum, 2007). This is a tendency to preserve the shapes of manual aiming movements even when the physical environment does not strictly require those shapes—for example, after moving the hand between targets having just moved the hand over an obstacle between two earlier targets (fig. 4.2). The hand moves higher after the obstacle than in a control condition with no obstacle. A similar carryover effect is shown in the time needed to prepare forthcoming response sequences. If the sequences preserve higher-order rules, the time to prepare them is less than if they do not. This tendency has been observed for language production (Bock, 1982) and tool use (Beisert, Massen & Prinz, 2010).

Collectively, the work summarized in this section leads to three conclusions about the serial order of behavior: (1) plans for forthcoming actions are represented hierarchically; (2) such plans are executed in a way that depends on their hierarchical organization; and (3) the plans are continually modified by changing the elements that are uncertain or that differ from what they were before.

The Degrees-of-Freedom Problem

Having considered two of the four problems of motor control—the perceptual-motor integration problem and the serial order problem—I turn next to the third of the four problems: the degrees-of-freedom problem. As mentioned before, this problem relates to the fact that an infinite number of possible solutions usually exist for any given task. The question of interest for students of motor control is which solutions are chosen and by what means.

Just as we considered pairs of thinkers who influenced early work on the perceptual-motor integration problem (Maxwell and Helmholtz) and pairs of thinkers who influenced early work on the serial order problem (Sherrington and Lashley), we can consider two thinkers who influenced the way we think about the degrees-of-freedom problem. They are Nikolai Bernstein (1896–1966) and Isaac Newton (1642–1727).

Bernstein and Synergies

Nikolai Bernstein was a physiologist who spent his career working in the Soviet Union. His work was published in Russian and was largely unknown to Western readers until the publication of an English translation of one of his books (Bernstein, 1967). His ideas were also brought to the attention of Western scholars by another contributor to this volume, Michael Turvey (1977).

Bernstein framed the degrees of freedom problem in terms of the indeterminacy of behaviorally relevant mappings. In perception (about which Bernstein said relatively little), any given proximal stimulus (e.g., a retinal image) can have many distal sources, meaning that the mapping of the proximal stimulus to those distal interpretations is one-to-many. For motor control, the problem is similar: For virtually any given task, there are an infinite number of ways of achieving the task. Again, therefore, the mapping is one-to-many.

Bernstein suggested that this problem can be solved by exploiting linkages. The linkages or couplings can exist between the external environment and the actor, and they can exist within the actor him or herself.

Such interdependencies have been studied in many tasks, including bimanual coupling, as discussed earlier in this chapter. The general notion is that the linkages may reduce the number of degrees of freedom that actually need to be controlled.

Newton, Mechanics, and Optimization

Turning to the other thinker whose ideas have impacted research on the degrees-of-freedom problem, Isaac Newton hardly needs an introduction here. He is famous for his laws of motion, referred to earlier in connection with Maxwell. Newton's postulation of the laws of motion is relevant to the degrees of freedom problem for motor control because, apart from the fact that all biological actions are subject to the laws of motion, those laws can be exploited by human and animal actors, reducing the degrees of freedom they would otherwise have to manage. For example, a baseball pitcher need not directly control all the features of his or her throw; physics can take care of the details. Other activities can similarly benefit from the exploitation of mechanics (Collins, Ruina, Tedrake & Wisse, 2005; van Ingen Schenau, 1989).

Newton not only developed laws of motion. He also developed calculus. Calculus is relevant to the degrees-of-freedom problem because it provides a way of finding maxima and minima (among other things). Being able to find maxima and minima can be critical for optimization. Bernstein did not stress optimization in his treatment of the degrees-of-freedom problem, but many motor control researchers subsequently pursued the optimization approach. The rationale for doing so, as first proposed by Nelson (1983) in the context of motor control, is to identify the best of the infinitely many possible ways of achieving a physical task. Here the word "best" means maximal with respect to some set of "good" values, or minimal with respect to some set of "bad" values.

The advantage of this approach is that it provides a way of finding a single means of identifying a task solution when neither classical mechanics alone nor linkages alone can do so. Being unable to rely on mechanics alone or linkages alone is common in everyday life. To cite one example, there are infinitely many ways to touch your nose. The method you normally use is more efficient than the methods that are physically possible but are never or rarely adopted. The unused methods are not ruled out by classical mechanics or by couplings, yet they are seldom if ever deployed, except perhaps to show that, as a result of voluntary control, one can touch one's nose in very strange ways (e.g., snaking one's arm over one's head). That one can do this at will is a nontrivial fact of motor control.

Optimization Constraints

A number of optimization constraints have been identified for motor control. The one that is best known and most historically influential is the minimum-jerk principle (Hogan, 1984). According to this principle, when an extremity is moved from one static position to another, the function relating speed to time over the duration of the movement tends to be bell shaped, symmetrical, and defined in such a way that the ratio of the peak speed to the average speed has a characteristic value. Apparently, positioning movements minimize the mean squared rate of change of acceleration over the movement time. The rate of change of acceleration (the fourth time derivative of position) is known as "jerk." Thus this proposed principle is sometimes called, colloquially, the minimum-jerk principle.

Not all experiments have supported the minimum-jerk principle, leading some investigators to ask whether it is a proxy for some other more general optimization principle. An alternative proposal is that movements actually minimize mean squared torque change—what might colloquially be called the minimum torque change principle (Uno, Kawato & Suzuki, 1989). Torque change is directly related to physical dynamics (forces and torques). Some movements satisfy the minimum torque change principle but not the minimum-jerk principle. At the same time, not all movements satisfy the minimum torque change principle. Which variable is minimized depends on the task, a crucial point that will be discussed later.

Optimization criteria have also been proposed for grasping objects. When people grasp the shaft of a standing toilet plunger, for example, they grasp the shaft at a place that depends on the height to which the plunger will be moved. If the plunger will be moved to a high location, it tends to be grasped low, but if the same plunger, standing at the same start position, will be moved to a low location, it tends to be grasped high. This inverse relation between grasp height and target height is linear over the range of start heights and target heights that has been tested (Cohen & Rosenbaum, 2004).

Why should this relation exist? If the shaft were always grasped at the same place no matter what the height to which it would be carried, the arm would end at an extreme joint angle at the low target and at an extreme joint angle at the high target. At extreme joint angles, power is reduced (Winters & Kleweno, 1993), proprioceptive sensitivity is reduced (Rossetti, Meckler & Prablanc, 1994), oscillation speed is reduced (Rosenbaum, van Heugten & Caldwell, 1996), and comfort (as reflected in numerical ratings) is reduced as well (Cohen & Rosenbaum, 2004). Therefore grasping

a shaft low for high placement or high for low placement avoids extreme joint angles when the final position is reached. Ending comfortably is not always observed, however. When more control is needed to lift the plunger from its home position, the shaft is grasped lower, closer to the position that affords greater control for the lift. This outcome—the modulation of where an object is grasped depending on what needs to be done with it—speaks again to the flexibility of performance depending on task requirements (Rosenbaum, Halloran & Cohen, 2006).

Such results are consistent with an optimization account, or more specifically with an optimization account that stresses sensitivity, comfort, control, and flexibility. Another factor that is important in planning is the challenge of planning itself. This claim is supported by another fact about grasping a plunger for movement to another location: after the plunger is brought to a target position and is returned to the home position after the participant has lowered her hand to her side, she tends to take hold of it where she let go of it before (Cohen & Rosenbaum, 2004). If sensitivity, comfort, and control were the only criteria for selecting grasp positions, participants would have grasped the plunger where it afforded the most comfortable position back at the home site. They didn't do that, however; instead they grasped the plunger where they held it before, returning it the home position, adopting, ironically, the same uncomfortable position they adopted there initially. This was not an artifact of the particular sites occupied by the plunger at its first and second site. When the initial and final positions of the plunger were reversed, the same pattern of behavior was seen. The interpretation given to this curious effect was that participants stressed physical comfort for the first move and then stressed computational convenience for the return move. In effect, participants "played the tape backward." The biomechanical cost of doing so was not disastrous for the return move, but the computational benefit, in terms of not requiring planning from scratch, was considerable.

The last point, regarding computational benefits, bears in an important way on classical optimization accounts of motor control. Those accounts typically do not factor in the cost of planning itself. Nevertheless planning does not come for free. Finding optimal solutions can take time and energy. This is one reason why it often suffices to find satisfactory rather than optimal solutions (Simon, 1955).

Defining and Redefining Criteria

As just seen in the previous discussion, if an object is first moved from one place to another, it may be most important to end the object displacement

with the arm near the middle of its range of motion; but if the object is returned to the place from which it came, ending the move with the arm at or near the middle of its range of motion may be less important than grasping the object where it was grasped before. Observations like this suggest that it is important to develop an account of motor control that is faithful not just to biomechanical constraints but also to psychological ones. A psychologically responsible theory of motor control must emphasize the task description as one of the most crucial loci of control by the actor. The idea is that what the actor elects to do given an ostensive task description comprises the core of his or her action planning. Deciding which criteria are more important than others is the essence of action selection. By extension, saying that any single criterion is always the most important one is probably misguided. The capacity to define and redefine action criteria is what permits actions to be as adaptive as they are.

The Learning Problem

Having said that changing criteria for performance is crucial for skill, it is possible to say that the way a skill is learned consists of appreciating what the skill's criteria should be. Learning to perform an ice-skating maneuver, for example, entails appreciating the sights, sounds, and feelings that should be strived for in order for that maneuver to occur. Likewise, learning to play a musical passage on the violin entails learning what perceptual consequences should follow.

This view of skill learning emerges from a theory of motor planning that my colleagues and I pursued (Jax, Rosenbaum, Vaughan & Meulenbroek, 2003; Rosenbaum et al., 1995, 2001), a theory that echoes, in important respects, claims made by others who developed theories of skill learning—notably, Adams (1971) and Schmidt (1975). The one aspect of our theory that distinguishes it from these earlier ones is the suggestion that motor acts are chosen with respect to *constraint hierarchies*. Constraint hierarchies are sets of prioritized constraints. Critically, the constraints' priorities change over the course of learning.

The constraint hierarchy is an attractive construct because of the kind of decision-making it affords. An effective way to choose an action is first to eliminate possible actions that fail to satisfy the most important constraint in the hierarchy, then to eliminate possible actions that fail to satisfy the *next* most important constraint in the hierarchy, and so on. This method, which is known as *elimination by aspects*, is efficient, especially when many constraints must be considered (Tversky, 1972).

A view of skill learning that follows from the constraint hierarchy perspective rests on the idea that a constraint hierarchy for a given task domain can change. After performing a task, an actor can make a determination about the extent to which different task features contributed to success. The constraint hierarchy can be adjusted accordingly: features that are found to contribute greatly to task success can be promoted; features that contribute less can be demoted.

This procedure can also lead to the discovery of new constraints. If during reliance on elimination of aspects, more than one possible action survives the winnowing process after all known constraints have been checked, just one of those remaining actions can be chosen at random. After such actions have been performed, if an incidental feature of the chosen actions is found to be more useful than was previously appreciated, that feature can be promoted, making it a true constraint rather than an incidental performance feature.

To the best of my knowledge, this is a new way of looking at skill learning, though it is certainly consistent with previous skill-learning theories and with what most skill learners and their coaches surely know—that it is important to be mindful of the most functionally relevant features of one's performance goals. Within this perspective, skill learning can be understood as being as much about perceptual learning as it is about motor learning. The last statement dovetails with the idea that action generation relies on perceptual representations (Hommel, Müsseler, Aschersleben & Prinz, 2001; Prinz, 1990). Curiously, their suggestion about the primacy of perception has had less impact on the study of skill learning than perhaps it should. The arguments offered here are meant to stimulate more contact of this kind.

Implications of the Constraint Hierarchy View

The constraint hierarchy view of skill learning has several implications. One concerns variability. Aspects of performance that are important should show little variability, whereas aspects of performance that are unimportant should show more. This idea has been pursued in connection with the so-called uncontrolled manifold (Scholz & Schöner, 1999). This is a performance dimension whose exact value, over some range, does not matter. By contrast, a performance dimension whose exact value over some range *does* matter is a (more) controlled manifold. Researchers have developed statistical tools to explore and test this idea. One approach has been to compare variability on different dimensions for tasks whose dimensions receive different emphasis.

A second implication of the constraint hierarchy view concerns what occurs after performance is over. According to the theory, after performance has occurred, the actor reviews the aspects of performance that led to success. This is needed, according to the arguments offered earlier, to determine the composition of the constraint hierarchy. A growing body of research indicates that the period after overt practice is extremely important for learning (Brashers-Krug, Shadmehr & Bizzi, 1996; Schmidt & Lee, 2005). A challenge for future research, then, will be to review the data about postpractice effects, viewing them from the theoretical perspective that constraint priorities may be adjusted during these times. A possible prediction is that the greater the extent to which constraints need to be reordered, the more time is needed between practice sessions.

Another implication of the constraint hierarchy view pertains to transfer. Transfer is a venerable topic in perceptual-motor skill learning, but one that has a bewildering range of results (see Schmidt & Lee, 2005, for review). It is possible that the constraint hierarchy view provides a useful way of accounting for transfer data. In general, it may be that the ease of transferring from one task to another depends on how similar their constraint hierarchies are. In addition, the way a task is performed may come to depend on the other task to which and from which transfer is required. That is, the way task A is performed when it is known that task B follows may be different from the way task A is performed when it is known that task B' follows. This would be expected if the system strives for minimal shifts in whatever constraint hierarchy occupies working memory. Data consistent with this view have already been reported for speech, where coarticulation effects are well known (Fowler, 2007), and for object manipulation, as reviewed earlier. I am making the prediction here for larger spans of behavior.

Yet another implication of the constraint hierarchy view is that coaching deserves a more prominent place in accounts of skill learning than it has received in the past. Coaches, according to the constraint hierarchy perspective, can direct attention to features of performance that their students should care about. Directing students' attention to important features of performance can speed the students' learning, obviating the need for exclusive reliance on trial-and-error promotion and demotion of constraints.

Finally, the constraint hierarchy account may help address a major question in skill-learning research, namely, what happens during the 10,000 hours or so of deliberate practice required to become an expert in a skill domain (Ericsson, Krampe & Tesch-Romer, 1993). Learning a skill may entail learning what constraint hierarchies are needed in which circumstances.

Perhaps the reason why practice needs to be deliberate is that cognitive resources are eaten up by monitoring the contribution of different features of performance to success and modifying the constraint hierarchy accordingly. If this hypothesis is correct, adding secondary, attention-demanding tasks should be especially detrimental when changes become necessary for the relative emphasis of different performance dimensions.

Looking Back

This section on the learning problem has pointed more to future challenges than to past accomplishments. The reason is that the perspective emerging from the earlier work that my colleagues have engaged in points to new directions for skill-learning research. I wanted to sketch those new directions here to keep the continuity of the ideas being advanced. Still, the present section would not be complete without an homage to two thinkers who helped set the stage for the general arguments made here. Those thinkers are Frederic Bartlett (1886–1969) and Charles Darwin (1809–1882).

Bartlett championed the idea of schemas, an idea that later became important in motor learning research (Schmidt, 1975). A schema may be defined as "a knowledge structure that can be instantiated in different ways depending on the values of its underlying variables or parameters" (Rosenbaum, 2010, p. 103). Bartlett argued for schemas because he believed they are used in recall. For Bartlett, recall is mainly reconstruction; seldom, in his view, is recall merely reproduction. For Bartlett, recall comprises an act of generating information, informed by, and often biased by, schemas brought to bear at the time.

Bartlett appreciated that the generative nature of recall applies as much to nonverbal action as it does to verbal action. He instantiated this perspective by discussing the preparation of a tennis stroke. Each tennis stroke, he said, is neither entirely old nor entirely new; instead it is an amalgamation of the two, an act generated on the fly, shaped by memory. Recognizing that action and cognition are of a piece, as Bartlett did, was prescient. His idea that memory is used to solve problems both for cognition and for action is a theme my colleagues and I have sought to promote in all our work.

Last but certainly not least, I mention Charles Darwin because he was one of the first to show the tremendous power of trial-and-error processes. Psychologists picked up on the idea, of course. Witness, for example, Edward Thorndike's (1927) famous work on the cat in the puzzle box. By

trial and error, the cat could manage its escape from the puzzle box more and more quickly in successive trials.

I have indicated that trial-and-error learning could be applied to the constraints that behaviors should satisfy. Via trial-and-error learning, it becomes possible to find out which features of performance should be promoted or demoted for a given task. Focusing on constraints provides a way of unifying perception and motor control because constraints must be evaluated in perceptual terms. Learning how to act more and more skillfully consists of learning what to care about and what not to care about (or to care about less). Focusing on constraints can, I believe, help us learn more about the control of action.

Conclusion

This chapter has summarized research on the planning and completion of physical actions. I discussed four problems: the perceptual-motor integration problem, the serial order problem, the degrees-of-freedom problem, and the learning problem. For each problem, I identified two seminal thinkers. I focused as well on research from my own laboratory. The justification for this focus is that my lab has been, arguably, the most avowedly mentalistic motor control lab in the world. The more my colleagues and I have delved into motor control, the more strongly we have been convinced that motor control is profoundly and fundamentally cognitive. The sense in which we mean this is that motor control is powerfully based both on memory for the past and on memory for the future (plans). I have tried in this chapter to convey the value of this approach, both with respect to results that have already been obtained and with respect to results that may be sought for the future.

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5 Ideomotor Action Control: On the Perceptual Grounding of Voluntary Actions and Agents

Bernhard Hommel

Introduction

"In the beginning was the act," Faust concluded in Goethe's (1808/1963) play of the same name, and this is pretty much the take-home message of the present chapter. Most theoretical accounts of the selection, planning, and control of human action follow the seemingly self-evident custom to begin their theoretical analysis with the stimulus, which is then taken to trigger, and to some degree "explain," action-related processes and the eventual execution of the action. Indeed, almost all textbooks of cognitive psychology and the cognitive neurosciences try to make us believe that humans are basically passive couch potatoes who are waiting for external events that make us get up and move.

In view of the experimental paradigms that cognitive scientists employ to investigate action-related processes and mechanisms, this idea seems to make perfect sense: the standard cognitive experiment uses stimulus presentation as the major means to control the experimental situation, and people's responses to those stimuli are considered the dependent rather than the independent variable under study. And yet the impression we get from our everyday life seems to suggest the exact opposite. Most stimuli we are exposed to are actually generated by our own actions: we smell the cologne because we have put it on our face, taste the marmalade because we dipped our croissant into it, laugh about the comedian's joke because we have switched on the TV, and so forth and so on. Thus we do not passively await stimuli to get us going but actively generate and seek the stimuli we intend to perceive. In the beginning is the act.

As argued by Hommel, Müsseler, Aschersleben, and Prinz (2001a, 2001b), the only historical tradition that has wholeheartedly embraced this theoretical perspective is the line of ideomotor theorizing. Ideomotor theory integrates several lines of reasoning and has a long tradition (Stock

& Stock, 2004; Prinz, 1987), which found its first systematic expression in the works of Lotze (1852) and James (1890). Given its emphasis on internal representations, it is not surprising that the approach fell into disgrace during the (from a cognitive perspective) dark ages of purist behaviorism, as exemplified by Thorndike's (1913) comparison of ideomotor theory with the animistic beliefs of underdeveloped tribes. But the approach did not fare much better in the most influential postbehaviorist manifesto of a cognitive psychology of action, Miller, Galanter, and Pribram's (1960) "Plans and the Structure of Behavior," where the authors reduced the intellectual contribution of ideomotor thinking to the (sometimes used) hyphen between "ideo" and "motor." However, the ideomotor approach regained some credibility through the work of Greenwald (1970) and others and now benefits from the positive press of theoretically related frameworks and concepts like embodied cognition and mirror neurons. In the present chapter, I briefly summarize the main assumptions of the Theory of Event Coding (Hommel et al., 2001a), arguably the most comprehensive ideomotor approach to date (for recent reviews, see Hommel, 2009; Shin, Proctor & Capaldi, 2010), and then turn to what I consider the most pressing theoretical questions to be addressed so as to validate this approach. In particular, I discuss whether agents do acquire action-effect associations in the way the theory suggests; whether agents really anticipate the perceptual effects of their actions, as the theory holds; whether these anticipations really control the action, rather than being a mere by-product; what aspects of an action these anticipations actually control; and, finally, what implications the theory and the processes it assumes have for the representation of the agent's self.

Ideomotor Action Control

The major aim of ideomotor theorizing is to explain how the cognitive representation of an intended action—an "idea"—can move one's body in such a way that the action is actually carried out, that is, results in motor activity. The original concept of the "ideo-" part was strongly connected to conscious representations (e.g., James, 1890), which, given the mainly introspective methods used by the early theorists, is not surprising. More modern approaches like those of Greenwald (1970) and Hommel et al. (2001a) tend to be agnostic with respect to the question of whether action goals do or do not require conscious representation to be effective, though some authors still feel that conscious representation is essential (e.g., Baars, 1988; for a review, see Hommel, 2007).

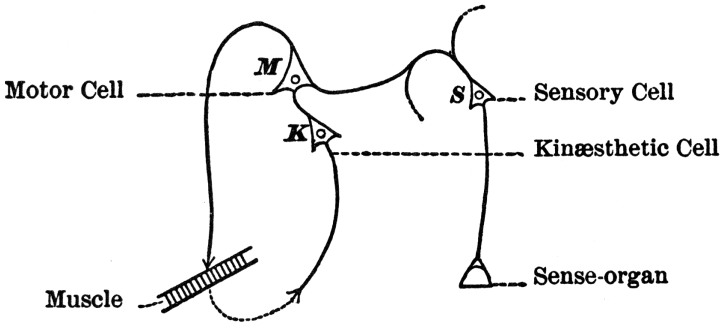

Figure 5.1
James's (1890) neural model of acquiring ideomotor control (see text for explanation). From James, 1890, p. 582.

The main mechanism underlying ideomotor action control has been nicely sketched in James's (1890) neural-network model (fig. 5.1). Here the hypothetical motor neuron M is assumed to move a particular muscle that, when being activated, produces kinesthetic feedback coded by neuron K. The more often this loop is active, be it through pre- or postnatal reflexes or random motor noise, or active exploration of one's own body and the world, the more often M and K will be concurrently active. Under the assumption that coactivation leads to association—which anticipates Hebb's dictum that "what fires together wires together" (cf. Greenwald, 1970)—this implies that M and K will become associated. Ideomotor theory holds that the association relating the two will be bidirectional, so that M can now be intentionally activated by endogenously activating K—that is, by "thinking of" the feedback that one may want to produce intentionally. The same scenario can be developed for any other sensory (visual, auditory, etc.) action feedback, so that M becomes coded in a multisensory fashion. If so, actively anticipating any sensory action effect will spread activation to, and thus gain control over, M, rendering the resulting action truly voluntary.

How Do Agents Acquire Action-Effect Associations?

According to ideomotor theory, voluntary action emerges through experience and the knowledge about the relationship between particular muscle movements and particular sensory effects that this experience allows one to acquire. Before having acquired this knowledge, the agent cannot have any idea about what outcome a given action might have. If we define intentional or voluntary action as a set of movements carried out to reach

a particular goal (which presupposes knowledge about expected action effects), this implies that action-effect knowledge turns aimless movements into voluntary action. This line of reasoning necessarily implies that the acquisition of knowledge about actions and their effects is involuntary and spontaneous; if volition is the result of action-effect learning, it cannot be its cause or precondition. In view of influential claims that question the existence of involuntary learning (e.g., Brewer, 1974; Shanks, 2010), it is thus important to ask whether the learning theory underlying ideomotor reasoning is tenable at all. Thus we need to ask whether action-effect acquisition is truly spontaneous.

Another challenge for ideomotor reasoning is its implicit assumption that motor patterns and codes of sensory action effects are associated in a bidirectional fashion. Clearly this assumption is necessary for the theory to work. In the scenario sketched in figure 5.1, the motor code M would usually be activated sometime before K, simply because K can only fire when M has passed some threshold to activate the muscle, which then needs to move before K is triggered. In the acquisition phase, the activation of M therefore always precedes the activation of K, which mirrors the external sequence of the movement and its sensory consequences. This scenario does not change if we assume that sensory action-effect codes may also be visual, auditory, and so on, as effects necessarily follow their cause. Intentionally producing the action, however, requires the use of the emerging association in the reverse direction: the codes of the sensory effects need to be activated to activate M and, eventually, the muscle. Intentional action thus requires the spread of activation from sensory codes to motor codes, which again requires the association between them to work either way.

One may consider this an odd assumption, as it implies that the information about the original sequence (first M, then K) is deleted from memory, at least at the representational level where action-effect associations are stored. Moreover, claiming that bidirectional associations exist seems to amount to assuming the efficacy of backward conditioning (i.e., acquiring a conditioned response to a conditioned novel stimulus that follows, rather than precedes, the unconditioned stimulus), which does not seem to fit with numerous failures to demonstrate this phenomenon (for a review, see Mackintosh, 1974) and theoretical claims that it cannot exist in principle (Pavlov, 1927). Accordingly, we need to ask whether action-effect associations are truly bidirectional.

Both of these questions have been addressed by adopting experimental paradigms from animal research (see Elsner & Hommel, 2001). In all versions, participants carry out particular actions, such as a left or right key-

press (R_1 and R_2), and are presented with novel sensory effects of these actions (E_1 and E_2), say, a low-pitched tone whenever they press the left key ($R_1 \rightarrow E_1$) and a high-pitched tone whenever they press the right key ($R_2 \rightarrow E_2$). Which key they are to press in the acquisition phase may be signaled by a discriminative stimulus (S_1 and S_2), as indicated in panel A of figure 5.2, or be left to their own choice (see panels B and C). The general idea is that the contingency and temporal contiguity between responses and action effects create bidirectional associations between their cognitive representations. If so, presenting an action-effect stimulus should prime the action that produced that stimulus in the acquisition phase.

Whether this is the case is tested in a subsequent test phase. In the study of Hommel (1996a), participants were still carrying out responses to stimuli, and the responses were still producing their effects (fig. 5.2, panel A). However, the actual stimuli were accompanied by task-irrelevant distractors that were similar to, or identical with, the effect of one of the actions. As expected, participants were faster to respond if the distractor was related to the effect of the correct response than if it was related to the effect of the incorrect alternative response. The disadvantage of this design is that this type of priming effect might reflect stimulus-effect learning, response-effect learning, or both. To distinguish between these two possibilities, Elsner and Hommel (2001) created two groups of participants that both went through the same acquisition phase (fig. 5.2, panel B). Both groups were now to respond to stimuli that were previously used as action effects, but the mapping of effect stimuli to responses differed. In one group, participants carried out the responses to exactly the same stimuli that these responses had produced in the acquisition phase (e.g., $E_1 \rightarrow R_1$ after having experienced $R_1 \rightarrow E_1$, $R_2 \rightarrow E_2$), so that these participants should benefit from the hypothetical bidirectional action-effect associations. In the second group, participants received the reverse mapping, so that they would now respond to a previous effect stimulus with the response that had previously produced the alternative action effect (e.g., $E_1 \rightarrow R_2$ after having experienced $R_1 \rightarrow E_1$, $R_2 \rightarrow E_2$). As expected, participants were much faster in the first group than in the second, which suggests not only that people acquire action-effect associations on the fly (as all action effects in the acquisition phase were task irrelevant, and learning them was not encouraged) but also that these associations are bidirectional—so that previous consequences of actions can now serve as effective primes of these actions.

The same conclusion can be drawn from another version of the action-effect learning paradigm. Elsner and Hommel (2001) also had participants carry out a free-choice task after undergoing the acquisition phase. Now

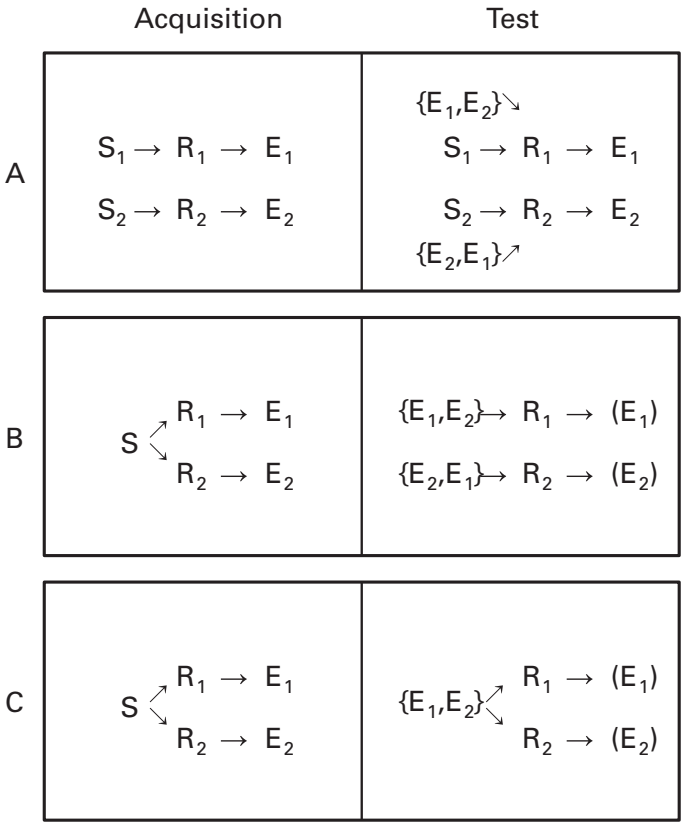

Figure 5.2
Experimental designs to investigate the acquisition of bidirectional action-effect associations. Note: S = stimulus; R = response; E = effect.

participants were presented with randomly selected action effects, which merely served as a trigger to carry out a self-chosen response (fig. 5.2, panel C). Ideomotor reasoning would suggest that the acquired action-effect associations would bias the selection toward the actions that were primed by the trigger stimulus. In other words, participants were expected to prefer the selection of the action that was previously producing the stimulus that was now serving as a trigger. This is exactly what Elsner and Hommel observed, irrespective of whether actions still produced their effects in the test case or not.

Numerous studies from various labs have demonstrated the spontaneous acquisition of associations between various sorts of actions and action-

contingent events from various sensory modalities (for a recent overview, see Hommel, 2009), suggesting that any kind of perceivable action effect can be learned. Elsner and Hommel (2004) provided evidence that the limits of action-effect learning are the same as for associative learning in general. In their study, participants acquired action-effect associations only if the temporal gap between action and effect was no longer than one second and if the relationship between action and effect was either highly contingent or if the effect occurred with a high frequency. The same limiting criteria have been reported from conditioning experiments in nonhuman animals, suggesting that the underlying integration processes are similar (see Elsner & Hommel, 2004). Likewise action-effect associations are not (much) affected by extinction, which is another characteristic that has also been reported from animal research (Rescorla, 1993). However, acquisition seems to set in much faster in humans than in other animals: Dutzi and Hommel (2009) reported that free choice is reliably biased toward the action that previously produced the current trigger stimulus after just one previous action-effect pairing.

Given the considerable developmental implications of ideomotor theory, it was important to demonstrate that its predictions do not hold only for adults but hold for children and infants, as well. Eenshuistra, Weidema, and Hommel (2004) translated the Elsner and Hommel (2001) paradigm into a child-friendly version and basically found the same effects in four- and seven-year-olds. In addition, four-year-olds exhibited a rather dramatic effect in the error rates (see also Kray, Eenshuistra, Kerstner, Weidema & Hommel, 2006), which suggested that at least some children were nearly or entirely unable to carry out an action to a stimulus that was previously produced by the alternative action. In other words, the behavior of the younger children seemed to be directly driven by (the representations of) action effects. Spontaneous and bidirectional action-effect integration could also be demonstrated in infants as young as nine months (Verschoor, Weidema, Biro & Hommel, 2010).

The observation that agents are picking up action effects even under conditions that do not provide any reward or benefit for attending to and learning them does not fit with suggestions of developmental researchers that intentionality precedes action-effect acquisition (Rochat, 2001). Rather, such findings support the ideomotor suggestion that intentionality emerges through experience. In other words, our action intentions are derived from the experience of options, rather than genetically given. However, though this scenario would elegantly address the long-standing philosophical question of where intentions come from (Lotze, 1852), it has been challenged

only recently. Herwig, Prinz, and Waszak (2007) compared two versions of action-effect acquisition paradigms: a forced-choice version in which, during the acquisition phase, responses were signaled by discriminative stimuli (as in panel A of fig. 5.2); and a free-choice version in which participants were only presented with a trigger and could select one of the two possible responses as they wanted (panel B). In the subsequent test phase (which was as in panel B), reliable effects of action-effect learning were obtained after free-choice practice but not after forced-choice practice. The authors concluded that action-effect integration relies on the degree of intentionality: In the forced-choice acquisition condition, people merely react to environmental demands, which does not lead to effective action-effect learning. In contrast, in the free-choice acquisition condition, people carry out actions to produce environmental effects and therefore consider action effects sufficiently relevant to acquire them.

If correct, this interpretation would for the most part undermine ideomotor theory. If action-effect integration would presuppose, rather than explain, the emergence of intentional action control, the applicability and theoretical range of ideomotor theory would be drastically narrowed, and the major strength of the theory would be eliminated. However, the intentionality hypothesis suggested by Herwig and colleagues is not without problems, and alternative interpretations are tenable. For one, reliable action-effect learning with forced-choice acquisition practice had been demonstrated before (Hommel, 1993, 1996a; Kunde et al., 2002), which does not seem to fit with the assumption that intentionality is necessary for action-effect integration and the assumption that stimulus-driven action is not intentional. For another, it may be that the reliance of performance on, and the resulting maintenance of, stimulus-response associations competes with the retrieval of action-effect associations. This possibility is suggested by a recent study of Pfister, Kiesel, and Hoffmann (2011). These authors replicated the basic design of Herwig et al. (2007) but replaced the forced-choice task in the *test* phase by a free-choice task. The study obtained reliable evidence for action-effect integration, and the size of this effect was no different from that observed after free-choice practice. This pattern does not support the assumption that the mode of action or intentionality during acquisition matters, but rather is consistent with ideomotor reasoning.

To conclude, converging evidence suggests that people at all ages acquire the sensory effects of their actions spontaneously and on the fly. Codes of these action effects become associated with the motor patterns that originally led to the activation of these codes. The resulting associations are

bidirectional, so that the intentional or nonintentional reactivation of action-effect representations leads to the priming of the associated motor pattern.

Do Agents Anticipate Effects of Their Actions?

Ideomotor theory assumes that actions are selected by anticipating their sensory consequences. This anticipation entails the activation of the representations of these consequences, which spread activation to the associated motor patterns. Incidentally acquired bidirectional associations between motor patterns and representations of sensory action effects provide sufficient knowledge for anticipating action effects, but the availability of information does not necessarily imply its effective use. Accordingly, we need to ask whether agents are actively engaging in anticipating the effect of their actions.

A first hint of at least some sort of active anticipation can be taken from research on the planning of complex and sequential actions. Numerous studies have shown that the time people take to begin an action or the first element of an action sequence increases with the complexity of the movement(s) (Henry & Rogers, 1960) and the number of movement parameters to be controlled (Rosenbaum, 1980), suggesting that selecting and planning a movement take the entire action into consideration. More direct evidence for the active anticipation of the sensory consequences of actions comes from Hommel (1993). Participants in the study carried out a task that was expected to produce a Simon effect (Simon & Rudell, 1967; for reviews, see Hommel, 2011; Proctor, 2011): they carried out left and right keypress responses to the pitch of a tone that was randomly presented through a loudspeaker on the left or right. Although the tone location was task irrelevant, responses were faster if the response location matched the location of the stimulus tone—the Simon effect. In one of the conditions, pressing a key produced a light flash on the opposite side, so that a left keypress triggered a right visual action effect, and a right keypress a left action effect. When participants were instructed to "press the left/right key in response to the low/high pitch of the tone," the standard Simon effect was replicated: a key was pressed faster if its location corresponded to that of the stimulus tone. However, when participants were instructed to "flash the right/left light in response to the low/high pitch of the tone," the effect reversed: now a key was pressed faster if its location did not correspond to the tone location. This means that participants must have coded their responses with respect to the sensory effect they intended to produce, so

that intending to press a left key rendered the cognitive representation of the action "left," but doing the same to flash a right light rendered it a "right" action.

Converging evidence for the active anticipation of action effects comes from studies on the so-called action-effect compatibility. As observed by Kunde (2001), spatially defined actions are initiated faster if they are followed by visual action effects that appear in the same relative location. Along the same lines, Koch and Kunde (2002) reported that participants are faster to vocally respond with color names if the responses trigger the visual presentation of the corresponding color word or color rather than an incongruent color word or color. Given that in both of these studies, the action effects were presented long after the response was initiated, the reaction time effects must reflect some sort of anticipation of the to-be-expected sensory consequences of the to-be-selected action.

Further evidence for active anticipation was provided by two recent ERP studies. Waszak and Herwig (2007) had participants acquire keypress-pitch associations before presenting them with an auditory oddball task, in which standard tones and infrequent deviants appeared. Auditory deviants produced a P3 component that was more pronounced when preceded by the response that was associated with the standard. Band, van Steenbergen, Ridderinkhof, Falkenstein, and Hommel (2009) had participants perform a probabilistic learning task, in which some keypresses triggered tones of a particular pitch in 80 percent of the trials and of another pitch in the remaining trials. Experiencing a less frequent action effect generated a so-called feedback-related negativity (Miltner, Braun & Coles, 1997), an ERP component that is commonly seen when negative feedback is presented. Both studies suggest that carrying out a particular response is associated with the expectation that the corresponding sensory consequences appear.

Finally, in a recent fMRI study (Kühn, Keizer, Rombouts & Hommel, 2011), participants were to switch between a manual binary-choice task (pressing a left versus right key) and a facial binary-choice task (assuming a kissing versus grinning expression). The type of action was precued on a trial-by-trial basis, and the preparation interval between cue and target presentation was analyzed. Preparing for manual action activated hand-related areas of the motor cortex and the extrastriate body area, which is known to mediate the perception of body parts. In contrast, preparing for facial action activated face-related motor areas and the fusiform face area, known to mediate face perception. These results show that preparing for a particular type of action goes along with activating the cortical area that

process the sensory consequences that this type of action produces—long before these consequences are actually perceived.

Do Action-Effect Anticipations Control the Action?

We have seen increasing evidence that people do not only acquire but actively use knowledge relating the motor patterns driving their actions to representations of the sensory consequences these actions are likely to have. However, it is possible that active anticipation serves other purposes than action control, so that we need to ask whether action-effect anticipation and action control are directly connected. Do we have evidence that anticipation plays a functional role in selecting and controlling actions?

An interesting hint to such a role comes from research on what has come to be known as Hick's law, which refers to the observation that reaction time increases with the number of possible response alternatives (for a recent review, see Schneider & Anderson, 2011). Leonard (1959) reported an interesting exception to this law with tactile stimulation, which allowed particularly efficient responding independently of the number of alternatives. Given that Hick's law is commonly taken to reflect greater demands on, or more competition related to, response selection as more action representations compete for execution (see Schneider & Anderson, 2011), Leonard's observation suggests that response selection can successfully be circumvented with tactile stimulation. In a follow-up study, ten Hoopen, Akerboom, and Raaymakers (1982) found that the deviation from Hick's law is particularly pronounced with tactile stimulation at a frequency that fits best with the sensitivity of the tactile finger receptors. If we consider that tactile, as compared to visual or auditory, stimulation maximizes ideomotor compatibility (i.e., the similarity between the sensory features of the stimulus and the sensory features of the expected action effect; see Greenwald, 1970), this pattern of findings fits exactly with expectations from ideomotor theory. Indeed, if selecting an action involves anticipating its perceptual outcome, the selection process should be facilitated more the more sensory features the presented target stimulus shares with this outcome.

If ideomotor compatibility facilitates response selection by providing the opportunity to delegate the selection process to the stimulus, one would expect that the choice of ideomotor-compatible stimuli helps to reduce or even eliminate processing bottlenecks that are related to response selection. Applying this logic, Greenwald (2003; Greenwald & Shulman, 1973) showed

that making stimulus-response relationships ideomotor-compatible leads to a dramatic reduction or the elimination of the commonly substantial processing costs associated with processing two tasks at the same time. Although researchers still debate how large and how general this effect is (e.g., Lien, Proctor & Allen, 2002), it is clear that response selection can be drastically facilitated through ideomotor compatibility. This provides evidence that the sensory consequences of performing an action play a role when selecting it for execution, which suggests that response selection considers codes that represent and thus predict these consequences.

Further evidence along these lines comes from Kunde, Hoffmann, and Zellmann (2002). They had participants carry out a task in which one of four possible responses was to be performed in each trial. A precue informed the participant about the correct response with a high validity, so that, unsurprisingly, reaction times were faster if the cue was valid than if it was invalid. Importantly, the responses triggered auditory action effects according to a 2:1 mapping, so that two responses shared the same auditory action effect. Results showed that responses following an invalid cue were faster if they shared their auditory effect with the cued response, which suggests that switching from one (primed or preselected) response to another was easier if the to-be-expected action effect was the same. Clearly this suggests that effect anticipations are considered in response selection. This conclusion has received further support from Paelecke and Kunde (2007). They had participants carry out two tasks and varied the time interval between the two stimuli (the stimulus-onset asynchrony), as well as the compatibility between responses and their experimentally induced sensory effects. Effects of the time interval and compatibility combined in an additive fashion, which, according to the so-called locus-of-slack logic (Pashler & Johnston, 1989), suggests that action-effect compatibility affects response selection.

If representations of action effects are related to the selection and activation of associated responses, one would predict that presenting a stimulus that resembles or is identical with a previously acquired action effect leads to the activation of brain areas that are involved in the motoric realization of actions. To test this prediction, Elsner et al. (2002) presented participants with an acquisition phase (as shown in panel B of fig. 5.2) before placing them in a PET scanner. During the scans, participants were monitoring a stream of auditory stimuli for a target sound, which was arranged to never appear during the actual scan. The auditory stream contained various portions of previously acquired action-effect tones, which allowed identifying brain areas whose activation varied systematically with the number of

effect tones in the stream. Two areas were identified: the supplementary motor area, which is assumed to house executable action plans, and the right hippocampus, which was likely to link the auditory information to motor structures. A more recent fMRI study could replicate this observation in a similar but more sensitive design (Melcher, Weidema, Eenshuistra, Hommel & Gruber, 2008). Taken together, these observations provide strong evidence not only that representations of action effects are related to the motor patterns that generate them, but that these representations are affecting and playing a functional role in response selection—most likely through priming the action that is associated with the intended effect.

Note that this scenario leaves open how a particular action effect becomes "intended." Although this is an interesting issue, ideomotor theory is a cognitive approach that aims to explain how intended effects are translated into overt movement, but not a motivational approach that explains why that particular effect was chosen to control the action. Along the lines of de Wit and Dickinson (2009), one might speculate that what we call an action intention is simply the action effect that is presently considered the most promising in terms of expected reward. In any case, however, it is certainly true that motivational issues have hitherto been insufficiently reflected in ideomotor theorizing.

What Aspects of Actions Do Action-Effect Anticipations Control?

The scenario that ideomotor theory suggests for how actions are controlled has a strong feedforward flavor: the outcome of a planned action is predicted in advance, and though some final check whether the predicted effect actually occurred seems to take place (Band et al., 2009), there does not seem to be much room or need for continuous online control. It is obvious that such a scenario is insufficient to account for all aspects of action control or, more specifically, for action control at all levels. Consider, for instance, the study of Prablanc and Pélisson (1990). Participants were presented with a spatially defined target that they were to touch with their index finger. Unbeknownst to the participants, the target was sometimes slightly moved while they moved their eyes, so that no participant was able to detect the movement. Even if the target was moved after the onset of the finger movement, the finger always moved straight to the final target location and did so without any hesitation or temporal delay.

Observations of this sort and many other related findings (for a review, see Milner & Goodale, 1995) strongly suggest that action control takes place at several levels. At one level, the general purpose and major outcome

of an action are determined, and general features of the actions are planned ahead (i.e., offline) while, at a lower level, online adjustments to environmental changes can be made as long as the action is under way (Glover, 2004; Hommel et al., 2001b). Action control thus integrates feedforward and feedback mechanisms. The feedforward mechanism determines the relevant aspects of the action and portions of the sensory effects that the agent actually intends to produce, whereas the feedback mechanism provides the remaining parameters based on the current environmental state of affairs. Obviously ideomotor theory has not much to contribute to the lower-level feedback mechanism but focuses on the higher-level feedforward mechanism. This particular focus is a logical consequence of the theory's historical heritage. As discussed earlier, the originators of ideomotor theory were interested in the link between conscious states and motor activity, and their main methods were logical reasoning and introspection. According to Milner and Goodale (1995) and Glover (2004), consciousness gets access to higher-level processes (or their products) only while lower-level online processes are not consciously accessible in principle. Considering this asymmetry, it makes sense that ideomotor theory is more interested in the former than the latter.

According to the original proposal of Milner and Goodale (1995), higher-level and lower-level mechanisms operate independently, a theoretical choice that, among other things, reflects these authors' claim that higher-level processes are restricted to perception, while lower-level mechanisms are devoted to action control. This conception ran into a number of problems, however. The problems that are of major interest for present purposes are theoretical. Because voluntary action can be defined as carrying out movements to reach a particular goal, it is essential that action control comprises of some sort of anticipation. As discussed in the introduction, aiming for a particular goal implies the anticipation of a particular effect, as well as the expectation that this effect will be produced by a particular type of movement. Whether this information is consciously represented or not need not be important, but it is clear that the information goes beyond the present state of affairs—a kind of projection into the future. It is difficult to see how this projection could be made without any memory about past performance, action-effect relationships, the relative efficiency of actions, and so forth. Hence action planning relies on memory (Dixon & Glover, 2004). However, the original action-control pathway that Milner and Goodale (1995) envisioned had no access to long-term memory whatsoever, which raises the question of how the pathway could be configured to choose one action over another, process action-relevant informa-

tion and ignore irrelevant information, and consider the final action goal when adjusting the ongoing action to environmental changes.

The alternative suggested by Glover (2004) and Hommel et al. (2001b) is to keep the distinction between high-level offline processes and low-level online processes but to include action planning as part of a higher processing level. This choice not only deals with a number of empirical problems with the original scenario (see Glover, 2004) but also acknowledges the obvious fact that at least some aspects of action planning are consciously accessible (Hommel, 2007). Moreover, it provides the opportunity to address an important gap in Milner and Goodale's (1995) original story, namely, the question of how the operation of lower-level online mechanisms is actually controlled and adjusted to the current task goal.

Figure 5.3 sketches a recent suggestion of how this question could be addressed (Hommel, 2010). The basic idea is that high-level processes (the ideomotor level, as it were) control lower-level sensorimotor processes by providing the basic structure of the action plan and by increasing the gain of output from sensory feature maps that provide action-relevant information

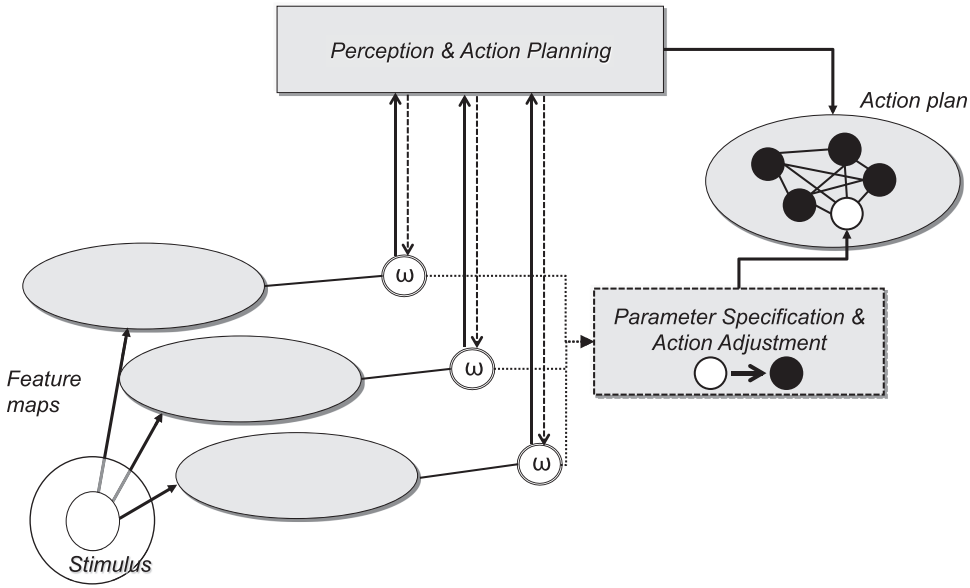

Figure 5.3
Sketch of a process model of the interaction between the offline-operating ideomotor perception-action system and the online-operating sensorimotor loop (see Hommel, 2010).

(Wykowska, Schubö & Hommel, 2009). Feature maps are assumed to code a given stimulus on different feature dimensions, such as shape, color, and orientation (Treisman, 1988), and to deliver that information to both higher-level processes busy with perception and action planning and lower-level processes that are continuously feeding environmental information into the sensorimotor loop. The perception-action system can increase the weight of information coming from action-relevant feature maps, such as the shape map in the context of a grasping action or the location map in the context of a pointing action. This increase will lead to a greater dominance of the corresponding information in the lower-level sensorimotor loop, so that the perception-action system can be considered to control the "attention" of the sensorimotor system. Moreover, the perception-action system will specify the goal-relevant features of the action, such as the object to be grasped or to be pointed to, but leave less relevant features, such as movement duration or hand posture (which, of course, may also be relevant under different goals), to be filled by the sensorimotor system.

This scenario implies interesting predictions that have been confirmed in a number of recent studies. Fagioli, Hommel, and Schubotz (2007) had participants plan (but not yet carry out) a reaching or grasping action before presenting them with a sequence of visual stimuli that did or did not include a size or location oddball. When participants had prepared a grasping action, they were faster to detect a size than a location oddball, while preparing a pointing action resulted in better performance for location than size oddballs. In other words, preparing an action facilitated the detection of visual stimulus features that can be assumed to provide the most relevant information for driving the sensorimotor loop underlying the action: the size feature for grasping and the location feature for pointing. The same conclusion is suggested by the finding of Wykowska et al. (2009) that preparing an action facilitates visual search for a pop-up target if the target is defined by an action-related dimension: size-defined targets benefit from preparing a grasping action, whereas luminance-defined targets benefit from preparing a pointing action.

As discussed in the context of the potency of ideomotor-compatible stimuli to facilitate or even circumvent endogenous action-selection processes, ideomotor theory suggests that external stimulus information can help or even replace endogenous action planning to the degree that it activates representations of (previously acquired) action effects. Access to motor patterns is assumed to be mediated through the activation of action-effect representations, and it does not matter in principle whether this activation stems from entirely endogenous processes or from external

stimulation—though in healthy adults, activation from endogenous processes will commonly be much stronger and more dominant than activation from external stimulation. If we combine this assumption with the idea that activating an action plan biases attention toward action-related features, it should be possible to achieve this bias even in the absence of endogenous action planning. To test that hypothesis, Fagioli, Ferlazzo, and Hommel (2007) used the same task as Fagioli, Hommel, and Schubotz (2007) but, instead of requiring participants to actively plan a grasping or pointing movement, presented them with short video clips that showed another person carrying out a grasping or reaching movement. Although these videos were not relevant to the task and did not predict the stimulus sequences or the correct response, participants were faster to detect size oddballs after having seen a grasping movement and location oddballs after having seen a reaching movement.

The Representation of Actions and Agents

Ideomotor theory assumes that actions are represented in terms of their perceptual effects, which renders cognitive action representations perceptually grounded in the sense of Harnad (1990). The same holds for representations of the agent himself or herself. According to the theory, it is only through the repeated experience of efficacy and the acquisition of action-effect associations that a random mover turns into an intentional agent. As actions are merely represented in terms of their reafference, so is the agent—one exists by virtue of making a perceptual difference. This perspective is very close to David Hume's approach to the representation of self. "I never can catch myself at any time without a perception," Hume (1739/1969, book 1, pt. 4, sec. 6) says, "and never can observe any thing but the perception. When my perceptions are remov'd for any time, as by sound sleep; so long am I insensible of myself, and may truly be said not to exist." This perceptual take on the concept of the self—the minimal self in the terminology of Gallagher (2000)—suggests that people, including oneself, are cognitively represented just like any other event: in terms of the perceptual effects they create. The cognitive representation of oneself would thus comprise a network of codes that refer to the sensory effects one has perceived to produce. A recent series of experiments on the so-called social Simon effect has provided evidence for this kind of perceptual grounding of the self.

As mentioned earlier, the standard Simon effect is observed when an agent carries out spatially defined responses to nonspatial stimulus features

appearing at randomly varying locations. If, for instance, a participant is to press a left and right key in response to a green and red stimulus, respectively, she or he will be faster and more accurate if the green stimulus happens to appear on the left side and the red stimulus on the right side (cf. Simon & Rudell, 1967). If this task is turned into a go/no-go task by having the participant operating only one of the two keys, the Simon effect is drastically reduced or even disappears (Hommel, 1996b), presumably because left and right responses need no longer be discriminated and spatially coded. As a consequence, the response code no longer matches or mismatches with left or right stimuli, so that spatial stimulus-response relations no longer matter. However, a full-blown Simon effect is obtained if the other key is operated by another person (Sebanz, Knoblich & Prinz, 2003), which has been taken to suggest that other people's actions are spontaneously corepresented and to reflect "the social nature of perception and action" (Knoblich & Sebanz, 2006).

The ideomotor approach provides an alternative and mechanistically more concrete interpretation of this observation. If the cognitive representations of "self" and "other" mainly consist of perceptual codes, there is no qualitative, but only a gradual, difference between "self" and another coagent. This difference is more pronounced than the social approach of Knoblich and Sebanz (2006) would have it, as some dissimilarity and therefore the means to discriminate between "self" and "other" always remain. Moreover, in contrast to the social approach, this perceptual-self hypothesis suggests that the degree of dissimilarity, and thus of self-other discrimination, can vary as a function of the number of features shared between me and a coagent.

First evidence that the social Simon effect can vary as a function of the perceived relationship between coactors was provided by Hommel, Colzato, and van den Wildenberg (2009), who obtained a full-blown effect if participants worked together with a coactor who was as friendly as they were themselves, but no effect if they worked with an unfriendly, aggressive coactor. Further evidence was reported by Hommel, van den Wildenberg, and Colzato (2011), who tried to modify the perceptual integration of self and other by means of Gestalt laws. Pairs of participants were performing a social Simon task side by side with an open or closed curtain between them (to manipulate the Gestalt law of common region) and while holding or not holding the same pen (to manipulate the Gestalt law of connectedness). As expected, the social Simon effect varied as a function of perceptual relatedness: it was reduced if the curtain was closed and increased by holding the same pen. No effect was obtained if neither manipulation sup-

ported perceptual grouping, which suggests that self- and other-perception are essential for corepresentation to materialize. Although this issue calls for more research, the available observations provide support for the ideomotor suggestion that the cognitive representations of self and other are grounded in perceptual experience.

Conclusion

From the findings presented here, we can conclude that people acquire bidirectional action-effect associations spontaneously, use the information actively to anticipate action outcomes, and select suitable actions through this anticipatory process—just as claimed by the ideomotor approach to action control. Ideomotor action control specifies the goal-related, intended aspects of actions and sets the stage for low-level online processes that take care of the further adjustments of ongoing actions to the environmental conditions. The ideomotor approach implies that actions are cognitively represented in terms of their sensory consequences, and action goals consider these consequences in formulating intended action outcomes. Thus people do not directly set up motor patterns to carry out movements, nor do stimuli directly trigger such patterns. Instead action planning seems to operate on perceptual representations that act as retrieval cues for goals and motor activity. In other words, action goals and action plans are not abstract mental constructions but truly perceptually grounded (cf. Harnad, 1990). From this perspective, perception serves action control, and one may speculate that the mechanisms that humans have developed to control perceptual processing —attention, that is—are a mere phylogenetic by-product of the need to optimize action control and the interaction between high-level planning and low-level sensorimotor processing in particular (Hommel, 2010). In that sense, Goethe might have been right: in the beginning was the act.

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II Ecological Approaches

6 Ecological Perspective on Perception-Action: What Kind of Science Does It Entail?

Michael T. Turvey

Introduction

Ecological psychology is a psychology for all organisms, the ninety-six phyla that make up the Five Kingdoms—Bacteria, Protoctista, Animalia, Fungi, and Plantae (Margulis & Schwartz, 1982/1998). Its focus is the question of how organisms make their way in the world (and not the more popular question of how a world is made inside of organisms) (Reed, 1996). Its goal is the scientific explanation of *agency*, the fact that all organisms manifest some degree of autonomy and control in their encounters (E. Gibson, 1994; Reed, 1996; Shaw & Kinsella-Shaw, 1988). Agency encompasses (i) variation of means to bring about an end (flexibility), (ii) coordinating current control with emerging states of affairs (prospectivity), and (iii) coordinating current control with prior states of affairs (retrospectivity). The agency of earthworms (animals with limited sensory organs and no discernible brain) provides a historically apposite example (Darwin, 1881). In plugging and lining their burrows, earthworms select leaves for substance and size, pulling each leaf into the burrow in ways specific to its shape. When the air is warm and moist, an earthworm's leaf choices are less selective. A persistent constraint on selection, however, is the size of the leaf relative to the size of the burrow's exit. When leaves are not available, then small stones are used for the same purpose. Earthworms are *aware of* their situation in this definitional sense: they perceive meaningful distinctions and organize their actions accordingly (J. Gibson, 1979/1986; Reed, 1996).

Commensurability of Psychology, Biology, and Physics

The ecological approach sees the traditional incommensurability of psychology, biology, and physics as a major barrier to understanding how

organisms make their way in the world—how they perceive and act. The matter-mind dualism (associated historically with Descartes) promotes two incomparable languages of exposition, one for matter and one for mind. In a classical variant, the physical language of light reflected to the eye is incommensurate with the mental language of the environment as perceived and acted on in grain size, number, variety, and types of descriptors. Theories of perception (and action) are charged, thereby, with identifying special processes sui generis that can translate between them.

The physics-biology dualism (associated historically with Kant) invites separate and distinct scientific accounts of inanimate and animate nature. The self-assembly of organisms, and the increase in their componential and functional order with evolution, development, and learning, are phenomena seemingly beyond the scope of the physics of matter and even contradictory to it.

What binds the two dualisms is the perspective that whereas inanimate things are seemingly inert and purposeless, animate things are most obviously active and purposeful. In *The Critique of Judgment* (Kant, 1790/2000), this self-causing nature of animate things led Kant to describe them as having "natural ends" or Aristotelian final causes and "inner purposefulness," and as such requiring teleological explanation. Organisms (and thus biology) were therefore at odds with physics, a field equated by Kant with the mechanics of Newton and Laplace.

The incommensurability of psychology, biology, and physics affects orthodox theory and research on perception-action. It encourages taking loans of intelligence and deters seeking explanation from first principles. "Loans of intelligence" is a phrase borrowed from Dennett (1981). It is used within the ecological perspective to refer to a theoretically undesirable presumption of intelligence to account for intelligence. Such loans, when taken, are not subsequently repayable within the conceptual framework that led to the loan taking. Internal models of Euclid's geometry and Newton's laws, and knowledge of how and when to apply them, are contemporary examples of intelligence borrowing. The act of expressing the geometry, laws, and rules of use as mechanisms (as computer algorithms) is not a repayment of the loan, as some might argue, but a mere currency conversion.

"First principles" is a phrase referring to something basic or foundational that is not deducible from something else. In physics, the laws of thermodynamics may be regarded as first principles. Arguably, they can provide a framework for addressing agency without intelligence borrowing (e.g., Kugler & Turvey, 1987; Swenson, 1999).

Perception

The prime requirement for the behaviors of living things at all scales is that perceiving provides a reliable means for orienting and adjusting activity to the environment. For an organism steering its way through the clutter of its surroundings, the question "to what does the organism's perceiving refer?" seems to demand the answer "that to which the organism's activity refers." The answer equates the proper "objects" of perceiving with the proper "objects" of activity (J. Gibson, 1979/1986; Turvey, Shaw, Reed & Mace, 1981). To be an "object" of activity is to be an aspect of the surroundings that entails activity. Examples for Animalia might include a stand-on-able surface, a fly-through-able opening, a cross-over-able gap, and so on. Expressed differently, the examples are a surface that affords standing on, an opening that affords passage, and a gap that affords crossing. In summary, the perceiving by the organisms of the Five Kingdoms, no matter how limited the perceiving may be, refers to *affordances*—activity-specific meanings of the surroundings. And insofar as behavior demands prospective (forward-looking) control, the perceiving of, or awareness of, activity-specific meanings amounts to perceiving or being aware of the possibilities for behavior and controlling behavior accordingly (affordance-based control; Fajen, 2007).

Figure 6.1a provides a synopsis of the preceding discussion. It contrasts the two-terms (or one-step) relation of the ecological approach to perception, so-called *direct perception*, with the three-terms (or two-steps) relation of nonecological approaches, so-called *indirect perception* (Turvey et al., 1981). The three-terms relation is epistemologically paradoxical. The two-terms relation is not.

Paradoxes

To make the point about the paradoxes, it will suffice to consider but one, the paradox of unconscious inference. Key to the variant of indirect perception promoted by Helmholtz (1886/2000, Vol. 3) is abduction, a form of inference that goes from observation to explaining hypothesis, from effect to cause. For example, if the observation (see fig. 6.1b) is "this thing is speckled" and the explaining hypothesis is that "all speckled things are cylinders," then the fact is "this thing is a cylinder." In abduction, as in induction, conclusions do not follow necessarily from premises. Abduction merely suggests that something *may be*.

Figure 6.1b is the man-in-the-inner-room metaphor cast in terms of Descartes's three grades of sense (in *Reply to the Sixth Set of Objections*;

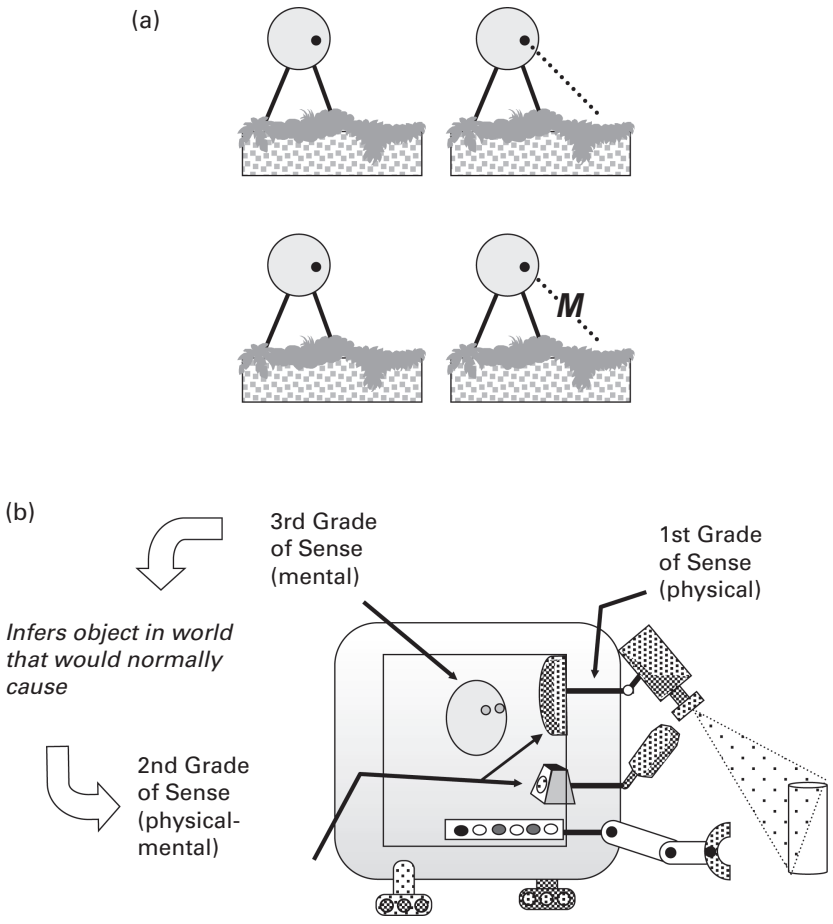


Figure 6.1
(*a*) The two-terms and three-terms relations. (*b*) Paradox of unconscious inference expressed through Descartes's trialism.

Haldane & Ross, 1911). Whereas the first grade is essentially material (e.g., physical processes occurring in eyes, optic nerves, and brain) and the third is essentially mental (e.g., reasoning), the second is a hybrid, neither essentially material nor essentially mental (the sensations). In Helmholtz's variant of indirect perception, judgments on the second grade of sense are mediated by unconsciously conducted (abductive) inferences.

Here is the paradox. In respect to figure 6.1b and a typical perceptual achievement, such as perceiving spatial reality, the knowledge necessary for unconscious inference is that of the connection between the second grade of sense (sensations) and the external spatial reality. Unconscious inference, however, is proposed as an explanation of how the outside spatial reality is known. This means that the third grade of sense must be endowed with knowledge of the connection between sensations and spatial reality before knowing about that reality through unconscious inference. In short, environmental causes (the *priors* in Bayesian formulations) and their relations to sensory effects must be known to implement unconscious inference. But they can only be known by unconscious inference. (This is not the only problem with the perception-as-abduction formulation, as fig. 6.2 highlights.)

Allowing license to generalize, questions forced by the paradoxes[1] are of the following kind: Why has philosophical and scientific inquiry into perception-action persisted with the three-terms relation? Why has it remained center stage in the lengthy history of theorizing about perception?

But questions should also be of the following kind: Why has the two-terms relation not come to the forefront? Why is it so elusive? In the present chapter, providing an answer to the latter questions is interpreted as providing an answer to another question: *what kind of science does the two-terms relation entail*?

Perception Is a State of Affairs

Within the persistent historical three-terms relation, perception is most commonly expressed as a form of reasoning or argument. Consequently it can be true or false, right or wrong, with no intrinsic basis for resolution. It cannot be a grantor of awareness of ecological reality. It cannot ground the origin, evolution, and agency of Bacteria, Protoctista, Animalia, Fungi, and Plantae. More narrowly, it cannot secure grounding of the "representations for" that is central to the theories fashioned within the three-terms relation.

Within the two-terms relation, perception's validity is by force of existence, not force of argument ("true," "false," "right," and "wrong" do not

The Riddle of Abduction
(Fodor, 2000; Rellihan, 2009)

How can abduction be mechanical (M) *and* feasible (F) *and* reliable (R)?

M = abduction is computationally implementable

F = modular components are informationally encapsulated
(constrained to current input and proprietary database, otherwise they will be non-terminating)

R = abduction is *un*encapsulated (no *a priori* basis for delimiting requisite variety and depth of knowledge needed for success)

The Riddle
abduction can be:
M and F only if not R
M and R only if not F
F and R only if not M

Resolution
F and R are non-negotiable, therefore *not* M

Figure 6.2
The "riddle" of abduction.

apply). Perception is a state of affairs and hence incorrigible (Shaw, Turvey & Mace, 1982; Turvey & Shaw, 1979). It can be a source of necessary a posteriori truths and, as such, can ground the agency of all phyla.

Textbook uses of the term "perception" tend to be species of "judge" or "decide" or "guess" that implicitly presuppose perception as an incorrigible state of affairs. To anticipate, the challenge of perception as a two-terms relation entails, at a minimum, a physics of complex adaptive material processes with an essential semantics component. What should this physics include?

Information About

One immediate response is that it requires a definition and a formal understanding of "information" as a scientific term that picks out an aspect of nature that is both law based and intentional (that is, *about* something). For Gibson (1966, 1979/1986), information is *information about in the sense of specificity to*. The argument is that, at all ecological scales, encompassing

the niches of all species in all phyla, there exist lawful relations between (a) niche properties meaningful to agency and the governing of activity, and (b) properties of structured ambient (optical, mechanical, thermal, chemical) energy distributions. Accordingly, (b) can specify (a). Determination of law-satisfying characterizations of (a) and (b) is an ongoing and far-from-complete enterprise, as subsequent sections will highlight.

Kugler and Turvey (1987, chap. 4) identified three decisive ideas behind the ecological conception of information. First, alternative descriptions in macroscopic kinematic (space-time), geometric (spatial), or spectral (temporal) terms, singly or in combination, can be given of the energy distributions, singly or collectively (see Stoffregen & Bardy, 2001), that envelop living things. Second, these alternative descriptions are law based and thereby determinate. Third, these alternative descriptions do not cause living things to move, ramify, grow, or spread—they are not forces or unconditioned stimuli—but provide the basis for reliably controlling behavior, for reliably realizing agency. Because information in Gibson's specificational sense is lawful, purposeful activity can, in principle, be conducted in all phyla in a consistently reliable manner.

The Challenge

The primary technical challenge of the ecological conception of information is identifying the physics and mathematics that capture its lawfulness and universality across phyla (and perforce across the multifarious means of registering it). In the case of visual perception, the ecological perspective's well-known effort to meet the challenge is the *ambient optic array*. This relational structure of nested optical solid angles, fully surrounding a point of observation and defined by differences of intensity in different directions, is founded on the basic understanding that light from a source (such as the sun or a lightbulb) is scatter-reflected or diffused by the faces and facets of surfaces (J. Gibson, 1966, 1979/1986). In the case of a layout of facing surfaces (consider, for simplicity, a furnished room), the consequence of scattering is multiple-reflection or reverberation, an endless bouncing of light from surface to surface, a network of convergence and divergence that is indefinitely dense. Multiple-reflection endows the light in the room with uniqueness. In Gibson's (1966) terminology, the uniqueness exists at the level of each pencil of light (a point in the room), at the level of the set of all pencils (the room itself), and at the level of each series of adjacent pencils (point-to-point translation within the room).

The ecological notion of the specification of the environment by light distributions is expressed in the foregoing terms. Where do the contemporary

physics and mathematics of reflected light stand in this regard? The first true theoretical efforts to address reflection from natural surfaces, that is, surfaces that are rough (technically not planar at all length scales), began in the 1980s. In the developing enterprise, "multiple-reflection" has referred to the scatter induced by a single one-dimensional surface or a single two-dimensional surface (for a review, see Maradudin & Méndez, 2007). In these contexts, "multiple" identifies the presence of many light "scatterers" or "diffusers," the nooks and crannies of a single surface. The single surface in itself is problematic. Theoretical studies of such (non-Gaussian random) surfaces are short on random functions for which the characteristic functional is known. Nonetheless insights are accumulating about the form that the new optical quantities should take.

The foregoing discussion provides the opportunity to underscore the magnitude of the challenge posed by ecological optics: the foundation for optical information in the specificational sense is the physics and mathematics of multiple-reflection by, and multiple reflection among, indefinitely many reflecting surfaces, each of non-Gaussian randomness that differs from surface to surface. These physics and mathematics are embryonic. The embryonic evaluation applies equally to ecological acoustics, ecological mechanics, and ecological chemistry—to the patterned energy dispersals that make possible perceiving by listening, touching, smelling, and tasting in all their manifest forms within the Five Kingdoms.

Action

A point of departure for the ecological perspective has been the Bernstein problem. At its core is the multiplicity of degrees of freedom (DF) participating in biological movement (Bernstein, 1967, 1996): how is a movement system's state space of very many DF compressed systematically into a control space of very few DF (Turvey, 1990, 2007)? What principles are entailed? What enables concinnity?

Concinnity in Animalia

Consider a human example. The act of speaking is very much a matter of concinnity, of adaptively fitting parts of the speech system to each other and to the speech system as a whole. The speech system comprises approximately seventy muscles, and the simplest utterance, for example, a consonant-vowel syllable such as /pa/, appears to involve all of them (Abbs & Connor, 1989). Respiratory movements of the diaphragm, rib cage, and abdomen, laryngeal movements of the trachea, thyroid, cricoid, and arytenoid cartilages, and articulatory (upper-airway) movements of the pharynx,

tongue, soft palate, lips, and jaw must be coordinated. The required concinnity of event timing in the respiratory, laryngeal, and articulatory systems for the simplest of utterances is demanding. This demand is much greater than that suggested by the division into three systems, however. The required concinnity is manifest simultaneously over multiple linkages among respiratory, laryngeal, and articulatory events. For example, producing the single gestural feature of bilabial closure—a feature that is concurrent with many other features in the production of a consonant such as *p*—involves coordinate activity in muscles of all three systems. Issues of sequencing speech piggyback on resolving issues of concinnity.

Concinnity and the Bernstein Problem in Other Kingdoms

Within Bacteria, 10^9 individuals comprising a colony act in a unitary manner, with individual bacteria adapting behaviorally and chemically to each other and to the colony as a whole, in achieving optimal resolution of contradictory constraints imposed by limited food in their sphere of activity (Ben-Jacob & Levine, 2006). Within Protoctista, the plasmodial slime mold, upon encountering several differently located food sources within its span, transforms from a high-dimensional protoplasmic streaming mode for transporting metabolites and oxygen to a low-dimensional (minimally possible) Steiner tree mode (Nakagaki, Kobayashi, Nishiura & Ueda, 2004). For all Plantae, stomata (the variable pores of plants with densities of tens to hundreds per mm^2) must be adjusted in size to maximize CO_2 uptake for a fixed amount of water loss. Stomatal adjustments are coordinated simultaneously at the level of adjacent patches within the individual leaf, at the level of the whole individual leaf, and at the level of the entire plant (Peak, West, Messinger & Mott, 2004).

Concinnity without an Orchestrator

The foregoing variants of concinnity seemingly imply a pure heterarchy—an organization without an organizer, concinnity without an orchestrator. A pure heterarchy manifests as a control principle of circular transitivity: if A modulates B and B modulates C, then not only does A modulate C but C modulates A and B modulates A. Concinnity is self-administered. *What kind of science does (self-)concinnity entail*?

Toward Commensurability: End-Directed Systems from Thermodynamic Laws

An enduring argument for the incommensurability of biology and physics is founded on a particular interpretation of the second law. If entropy

increases in all natural processes, and if entropy production is equated with disorder, then biological systems, their evolution and their development, are orthogonal to thermodynamics. This argument owes much to the emphasis of nineteenth-century and early twentieth-century thermodynamics on linear dynamics, equilibrium systems, and reversibility. A contrary argument is founded on the fuller understanding of the second law pursuant to the contemporary emphasis on nonlinear dynamics, nonequilibrium systems, and irreversibility (Kondepudi & Prigogine, 2004). The fuller (deeper) understanding is that *entropy-producing irreversible processes create order*.

Appreciation of the second law's constructive role requires a prior appreciation, namely, that the second law as originally formulated is a statement of final cause in the Aristotelian sense of the end to which everything strives and everything serves. The first law tells us that all energy forms are interconvertible with the total energy invariant over the varied interconversions. It expresses a symmetry (invariance over time translation) governing physical laws. The second law also expresses a symmetry, but one that is unfulfilled (Swenson & Turvey, 1991). To the extent that energy distribution is not uniform, the second law "strives" to render it uniform. In short, contrary to the assumption of a purposeless physical world derived from mechanics, the second law of thermodynamics tells us that the physical world is end driven. The end state is maximum entropy (or minimal availability of energy to do work, or maximum dissipation of resources).

The significance of irreversible processes and the second law to biological systems and their characteristic properties (e.g., agency, perception-action) is therefore twofold. First, order from disorder and more order from less order are inexorable consequences of a universal symmetry principle. Second, the same universal symmetry principle guarantees the necessary precondition for evolution by natural selection presumed by Darwin—purposive entities dissipating resources. No special ad hoc principle need be invoked or, indeed, can be invoked legitimately (such as *teleonomy*, the attribution of end directedness through a program).

A Further Principle

Although the second law of thermodynamics tells us that entropy is maximized at thermodynamic equilibrium, it is mute on the issue of the path taken to that end. A further universal principle of path selection is implicated. Figure 6.3a–c schematizes the classic empirical example of emergent order and (self-)concinnity (the surface-tension-driven Bénard convection

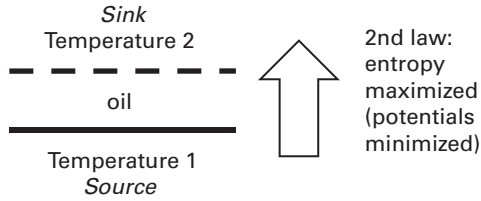
instability; see Koschmieder, 1993), and figure 6.3d displays, in sequence, time slices of the evolution from the unordered, to the locally ordered, to the intermediately ordered, to the fully ordered state. For the second law to remain inviolate, each transformation in this sequence must be accompanied by an increase in the rate of entropy production.[2] That said, the issue is then to understand why such transformations should occur, and why they should occur whenever the opportunity arises. Seemingly the answer must be that the reduction of potentials or gradients demanded by the second law abides by a rate principle: for a given opportunity (circumstance), the world is in the business of degrading potentials at the fastest rate afforded by the given opportunity. This principle has been referred to as the Law of Maximum Entropy Production (LMEP) (Mahulikar & Herwig, 2004; Swenson, 2010; Swenson & Turvey, 1991).[3] It can be advanced as the fourth law of thermodynamics (see the discussion in Martinez-Kahn & Martinez-Castilla, 2010). It permits a large step to be taken toward commensurability of psychology, biology, and physics.

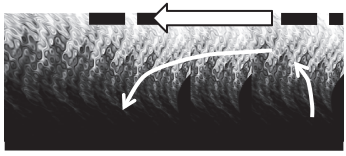
Perception-Action and First Principles

In perceiving-acting, organisms hook their onboard energy reservoirs to the invariants of ambient optical distributions, compression wave fronts and wave trains, fields of diffusing volatile materials, and so on. The consequence of being able to do so is that organisms can search for, find, and consume energy depots at many nested lengths and timescales, thereby expanding the earth's dissipative space and increasing the global rate of entropy production (Swenson & Turvey, 1991). Perception-action in its multiple manifest forms within the Five Kingdoms has a deep and direct connection to thermodynamic principles.

Returning to figure 6.3, panels (a) and (b) detail the emergence of an autocatakinetic (ACK) system.[4] Panel (c) identifies the functional composition of the surface-tension-driven Bénard system expressed through panels (a) and (b) and, in so doing, provides schematically the requirements of ACK systems in general. An ACK system persists only as long as the formative potential persists (θ_1 in fig. 6.3c). Within that constraint, it might be able to take advantage of other potentials, some proximate, others not so proximate. In terms of deriving perception-action from first principles—from thermodynamics—a major unmet challenge is that of understanding how an ACK system becomes coupled to energy distributions qua information about. It is that coupling that makes possible prospective control, an essential aspect of agency and a requirement for searching out nonproximate potentials.

a)





Heated substrate

Heated substrate

b)

c)

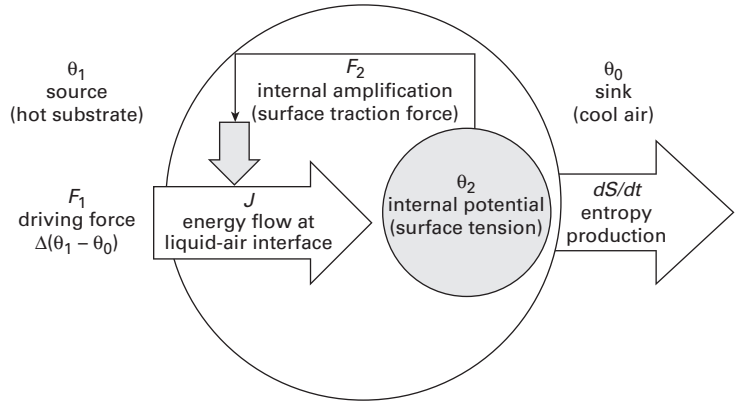


Figure 6.3
The surface-tension-driven Bénard convection instability. (*a*) Thermal flow from heated substrate (source) to liquid surface (sink) at air temperature. (*b*) Fluid motion is driven from the liquid-air interface. Spatial variations in the interface's temperature lead to gradients in the surface tension that drive motion in the underlying fluid. Liquid is pulled from warmer regions to cooler by higher surface tension of cooler regions. (Lower left is adapted from fig 3.2, p. 42, of Manneville, P. "Rayleigh-Bénard convection: Thirty years of experimental, theoretical, and modeling work," in I. Mutabazi, E. Guyon & J. E. Wesfreid [Eds.]. (2006). *Spatio-temporal cellular structures: Henri Bénard centenary review*, with kind permission from Springer Science+Business Media. Lower right is adapted from http://www.physics.utoronto.ca/~nonlin/thermal .html.) (*c*) At a critical source-sink temperature difference, the bulk fluid movement evident in (*b*) becomes structured as a series of small cells (Bénard cells), each cell comprising $\approx 10^{21}$ molecules, and each cell rotating in a direction opposite to its immediate neighbors. (*d*) The evolving convection (Bénard) cells viewed from above. (*i*) Incoherent motion at the microscopic level leads to homogeneity at the macroscopic level. (*ii*) Two cells emerging within an instant of the fluid becoming fully cellular. Because each cell arises from fluctuations, the first emerging cells will never repeat in location and order from one run of the experiment to the next. (*iii–iv*) The developmental process leading to a time-independent organization of regularly arrayed hexagonal cells entails spontaneous fissioning of cells and competitive exclusion. (Combination of figures 2, 4, and 5 from Swenson, R. [1989]. Emergent attractors and the law of maximum entropy production: Foundations to a theory of general evolution. *Systems Research*, *6*, 187–197, with permission of John Wiley and Sons.)

Toward Commensurability: Impredicative Entailments

Resolving incommensurability of biology and physics in the preceding section required recognizing that essential biological qualities follow from, rather than oppose, the most fundamental of physical principles. In the present section, incommensurability is approached from the other direction. Its premise is that animate systems are more general in respect to the physical principles that they express than the inanimate systems whose study has constrained physical theory to date. The premise's leading proponent is Rosen (1991, 2000).

Impredicativity and the Flow of Entailment

Inherited from the machine perspective on biology (caricatured in fig. 6.1b) is the direction of entailment regarding components and functions. From the machine perspective, entailment flows from component C to function F, $C \rightarrow F$. The examples of concinnity (or synergy) given earlier suggest, however, that the entailments for biological systems are closed

loop, of the form $F \rightarrow C_i \rightarrow F$, where C_i is inherited from F, and F is inherited from C_1, C_2, . . . C_i . . . C_k. The parts inherit their functions from the whole that they compose. In more general terms (paralleling Rosen, 1991, p. 121), a component can by its very nature have no completely inherent, invariant description that entails its function; on the contrary, its description changes as the concinnity to which it belongs changes (Turvey, 2004b).

Entailments that are closed loop—such as those of a concinnity, such as those of the surface-tension-driven Bénard system and of ACK systems in general—are identified as nonpredicative or impredicative. Whereas a predicative definition of something is context free, an impredicative definition of something depends on the totality to which it belongs.

Non-Well-Founded Set Theory (Alias Hyperset Theory)

A useful tool for impredicativity and its implications is non-well-founded (NWF) set theory (Aczel, 1988). Standard set theory is well founded in two senses: its implementation does not lead to paradoxes (it is logically well founded), and its graphs contain no infinite cycles or loops. In graph theory, every set determines a treelike graph in which the set itself is the uppermost node and each member of the set is a descendant node with an arrow pointing to it from the original set of which it is a member—an operation that is applied recursively. Aczel (1988) proved that a graph is free of cycles or loops *if and only if* the graph is well founded. A graph containing cycles or loops depicts non-well-foundedness. It indicates that the set has itself as a member, that the thing it graphs (a system or a concept) is impredicative. As presaged earlier, and as noted by mathematical logicians (e.g., Barwise & Etchemendy, 1987) and others (Chemero & Turvey, 2007, 2008; Kercel 2003), many real-world systems and concepts are circular and therefore illegal by the criteria of standard set theory.

Complex versus Simple

In a word, the central issue for Rosen (1991, 2000) is *complexity*. Whether a system is complex depends only secondarily on the system itself. Its primary dependence is on the system's models. A material system is *complex* if and only if it has irremovable impredicativities and therefore only impredicative models; otherwise the system is *simple*. The tools of NWF set theory help to make the distinction (e.g., Chemero & Turvey, 2010).

Edging toward Commensurability

The Rosen thesis at the core of this section is that scientific appreciation for the causal entailment of biology can only be achieved through impred-

icative means.[5] Impredicativity and the complexity of the inhabitants of the Five Kingdoms go hand in hand. But the Rosen thesis proposes, synonymously, that the physical principles needed to express the animate are the more general principles. The physics of living things nest the physics currently at our disposal. Biology is not incommensurate with physics. These conclusions are to be included in the larger lessons that Laughlin and colleagues—in their defrocking of "the theory of everything" (Laughlin & Pines, 2000) and their advocacy of "the middle way" (Laughlin, Pines, Schmalian, et al., 2000)—would like us to learn.

Back to Action Possibilities: The Affordance Hypothesis

A primary goal of evolutionary ecology is to provide descriptions of the surfaces and substances surrounding an organism that (a) capture uniquely the organism's fit to its surroundings, and (b) clarify how any given habitat (*where* an organism lives) is partitioned into distinct niches (*how* an organism lives). For the ecological perspective on perception-action, the base descriptor meeting this goal is *affordance*, a way of addressing surfaces, substances, and media in a manner that is directly relevant to the conducting of behavior (J. Gibson, 1966, 1979/1986, 1982). In respect to all five kingdoms, an affordance is an invariant combination of properties of surface, substance, and medium taken with reference to an organism and specific to an action performable by the organism.[6]

Theoretical and empirical work is guided by the *affordance hypothesis*: an organism's environment consists of possibilities for action, and is perceived as such. As an organism moves with respect to its surroundings, some action possibilities persist, some newly arise, and some dissolve, though the surroundings analyzed classically as objects and the geographic relations among them do not change. A change of pace or a change of location by a quadruped can mean that a break in the ground now affords leaping over, whereas at an earlier pace or location it did not. The environment-for-the-organism is dynamic and action oriented, while the environment-in-itself, that which has been the target of conventional theorizing, is fixed and neutral with respect to the organism and its actions (Turvey & Shaw, 1995).

Perceiving Action Possibilities

The number of experiments on affordance perception by humans (adults, children, and infants) is substantial.[7] Here, emphasis is given to select observations of other species of Animalia and one of Plantae. They augment the earlier review of Darwin's worms.

Limpet (Mackie, 1970; Branch, 1979). When preyed on by whelks and starfish, specimens of *Patella oculus* and *Patella granatina* either retreat or attack. (They can crush potential predators with their shells.) The relative limpet-to-predator size at which a potential predator is perceived as attackable rather than retreat-from-able is predator specific. It is smaller for whelks than for starfish.

Ant (Fellers & Fellers, 1976). Upon finding liquid foods, *Myrmicine* ants use leaves to absorb the liquid and as a cohort carry them back to the nest. Given the option of using leaf segments or mud chunks of equal size, they select the mud chunks. Liquid food is disposed to adhering to mud chunks, and mud chunks afford easier carrying.

Jumping spider (Tarsitano & Andrew, 1999). A food item is located at a site 11 mm above and 200 mm directly in front of the location of a participant from the genus *Portia labiata* (about 5 mm in length). The food is reachable by taking either one of two routes. When one of the two routes is made impassable by introducing a gap, *Portia* takes the intact route that affords locomotion to the food. *Portia* does so directly subsequent to visual inspection from its starting location, first of both routes, then only of the complete route.

Lizard (Moermond, 1979; Irschick & Losos, 1999). Analyses of what *Anolis* perceives as a branch on which to perch reveals that the following nexus of surface properties must be satisfied. The branch must be view-from-able (in respect to seeing both prey and predators), must be jump-off-able with accuracy, and must be sprint-on-able with maximal speed. These defining properties relate to the lizard's leg length and the branch's breadth and texture.

Seedlings (Kelly, 1992; Runyan, Mescher & De Moraes, 2006). On making contact with a host plant, a seedling of the parasitic genus *Cuscuta* (dodder) must perceive the nutritional value of the host before exhausting its energy reserves (it is nonphotosynthesizing) and before it "commits" to the host as an energy supply—that is, before it attaches to the host. Potential hosts vary in ingestible nutritional quality, and specimens of dodder perceive the differences, attaching with greater frequency to hosts of higher quality. Odor plumes diffusing from potential hosts carry information about the chemical value, what a host affords nutritionally.

Geometrical Empiricism and the Issue of the Kind of Science That It Entails

Implicit in the ecological perspective's functional interpretation of environment is the notion that a geometry undergirds perception-action capabilities and their study—a geometry that is grounded in material facts at

the level of ecology, the level of organism-environment systems. The mathematicians of the early nineteenth century (notably, Gauss, Lobatchevsky, and Bolyai) realized that Euclidean geometry was unfounded in the absence of an additional axiom about parallelism. This realization opened the door for the creation of a new set of axioms obtained by merely adopting a contradictory stance on the fifth postulate. The upshot was a variety of non-Euclidean geometries, each self-consistent, each as equally rigorous as the next, and all apparently able to describe space as thoroughly as Euclidean geometry (Cassirer, 1950; Kline, 1980). Gauss took a giant step and proposed that geometry be relegated from the comfortable heights of pure reason to the grind of empirical science: "Space has a reality outside the mind whose laws we cannot prescribe *a priori*" (Cassirer, 1950, p. 37).

An empirical geometry can take a benign form. Euclid's conceptual basis can be preserved intact with the critical issues limited to the kinds of experiments that would distinguish between Euclidean geometry and non-Euclidean geometry in respect to whether one represented space better than the other (Wagner, 2006). The general development of this form of geometrical empiricism is limited by the fact that Euclidean and non-Euclidean geometry are equally distant from ecological reality. For Cassirer (1950), the problem, simply, is that neither involves entities that can be experimented on. A truly empirical science of geometry befitting perception-action begins with (a) collecting, systematizing, and testing observations on the material layout of the environment, and (b) questioning Euclid's foundations—his abstract geometric elements of point, straight line, and plane—because of their tenuous connection to observable facts. Pasch (in Cassirer, 1950) sought to show in detail what an empirical geometry must be like and how it might be constructed without abandoning the rigor expected by either geometry or science. In so doing, he argued that although Euclid's elements can be derived from observable facts by idealization (limit processes), this idealization—its necessity and legitimacy—is at issue. Euclid's elements are not physically grounded.

The ecological perspective's concern with grounding the elements of geometry in the observable facts of the environment is evident in Gibson's (1979/1986) contrast between the abstract geometrical notion of *plane* and the ecological notion of *surface*. The surface, not the plane, is appropriate for the study of perception and behavior. Referring "space" to possibilities for action (affordances) is a furthering of geometrical empiricism, a step toward a characterization of "space" befitting the facts of perceiving-acting entities. Table 6.1 shows a summary of proposals, past and present, bearing on the intent and form of the notion of space (Turvey, 2004a). They can

Table 6.1
Notions of space pertaining to geometrical empiricism and ecological geometry

Proposal		Proponents
1.	Space as suggested by conditions of successful visually guided action, not by abstract geometry.	Berkeley
2.	Geometry of space as a posteriori, not a priori.	Riemann, Lotze, Helmholtz
3.	Space as space-for-agent, not space-as-is.	Kant, von Uexküll
4.	Space as dependent on its constituents, not absolute and container-like.	Riemann, Clifford, Einstein
5.	Space as local and intrinsic, not global and extrinsic.	Gauss, Einstein
6.	Spatial forms as primarily irregular and fragmented rather than regular and connected.	Mandelbrot
7.	Geometric elements as referring to material facts, not idealization.	Pasch
8.	Visible properties as signifiers of types of environmental contact, not as mathematical entities.	Berkeley
9.	Properties of space as relative to transformations of space, as relative to degree of free mobility.	Helmholtz, Klein

be taken as an evolving context of ideas for the development of an ecological geometry of surface layout, a process in which theory and experiment necessarily proceed hand in hand.

Back to the Two-Terms Relation: In What Sense Are Affordances Objective, Real, and Physical?

A historical division of some significance to addressing this question is the division between primary properties as the topic of physical science and secondary properties as the topic of a very different form of inquiry, namely, psychology. It helps to get as clear as possible on this division (a variant of incommensurability) and its interpretation because affordance theory is, at bottom, a theory of properties that are mutual to organism and environment, properties that have the look of secondary properties. It is worth underscoring that the historically predominant three-terms relation governing theorizing derives its sustenance from the conjecture that (in vision) sensations of color and brightness, secondary qualities, are the data (the *M* in fig. 6.1a) from which visual perception of the environment is inferentially derived.

On Predicating Properties

For the most part, science since Galileo has been comfortable with the notion of *intrinsic* property. On examining a substantial thing in the environment, say, a stone, the scientist presumes that it has properties that are internal to it, traits that have nothing to do with how they will be observed and measured. When an intrinsic property of the stone has been isolated to satisfaction, it is represented in the scientific formalism by a *concept*, *attribute*, or *predicate*.

In the framework of classical mechanics, predicating "mass" of the stone is intended to identify a substantial property intrinsic to the stone that is the same whenever and wherever the stone is observed. To predicate "velocity" of the stone when the stone is a projectile is slightly more complicated. The property in question is of a pair of substantial things, the moving stone and a reference frame. That is, the predicate "velocity" picks out a *relational* property (Bunge, 1977). For Galileo, and for science since his time, relational properties qualify along with intrinsic properties as *primary* properties under the following proviso: the property of any substantial thing *A* is expressed by, but not actualized in, its relation with another substantial thing *B* (Gomatam, 1999). If the *actualized in* clause prevails, then the property is *secondary*. Thus to predicate "velocity" of the stone is to refer to a primary property, but to predicate "gray" of the stone is to refer to a secondary property. The stone's color is actualized in the stone's relation to a perceiver.

Importantly, a stone enters into other relations, not involving perceivers, in which a property of the stone, one might argue, is both expressed and actualized (Gomatam, 1999). For example, when a stone is placed on a pile of papers, we predicate "paperweight" of the stone. Similarly, when the stone is positioned at the foot of a door, we predicate "doorstop" of the stone. Before setting up the appropriate spatiotemporal relations between the stone and the pile of papers and between the stone and the door, "paperweight-ness" and "doorstop-ness" are, respectively, potential properties of the stone. They become physically real only when the spatiotemporal relations are in place. It should be observed that, from a conventional viewpoint, these relational properties of the stone might still qualify as objective properties in that they are expressed in relation to nonliving things.

There are other relational properties of like kind, however, which do engage living things. For example, when a stone is grasped and brought down hard and repetitively on another object, one can predicate "hammer"

of the stone. Similarly, when a stone is grasped and scraped across the surface of another object, one can predicate "scraper" of the stone. Patently, these predications implicate a perceiver-actor. But is subjectivity also implicated? The requirement "graspable" for the stone to be a hammer or scraper means that a primary property of the stone, namely, its size, must be commensurate with the same primary property of the perceiver-actor's grasping system, the hand width. Objectivity, not subjectivity, is implicated.

Conceivably, a stone might have many relational properties by virtue of its relation to either other objects or perceivers-actors, but those properties are, at best, indefinite properties until a particular spatiotemporal relation is effected. When that happens, one of the many potential relational properties of the stone is actualized without compromising the others. That is, when a stone becomes a "hammer," for example, it is still potentially a "scraper," just as when an electron becomes an "up" electron it is still potentially a "down" electron. We can imagine that Galileo, Boyle, and Newton would have asked the following methodological question: in what settings do relational properties of the kind identified here arise in such a way that they could be of significance to the development of physical science? As is well known, physicists in the twentieth century encountered phenomena in relational settings that forced them to consider a possibility that would have been unthinkable to their seventeenth-century predecessors: *nothing is real (that is, definite) until it is measured* (that is, placed into a particular spatiotemporal relation with a meter or measurement device). If an object with its primary properties of mass, position, and velocity is always in only one of its logically possible states, and all variables composing a state have determinate values at all times, whether measured or not, then the aforementioned possibility is unthinkable. What made that possibility thinkable were the discoveries and interpretations that constitute quantum mechanics.

Affordances Are Objective, Real, and Physical in Quantum Compatible and Impredicative Senses

Figure 6.4 depicts an affordance, the relational property of jump-up-on-able. To say, with respect to figure 6.4, that the post affords jumping on for the squirrel is to recognize that it is (a) *expressed by* a relation with another object (like a classical primary property), and (b) *actualized in* relation to another object (unlike a classical primary property). Regarding the question, therefore, of what kind of science is needed to investigate affordance theoretically and experimentally, an answer of the following form can now be proposed.

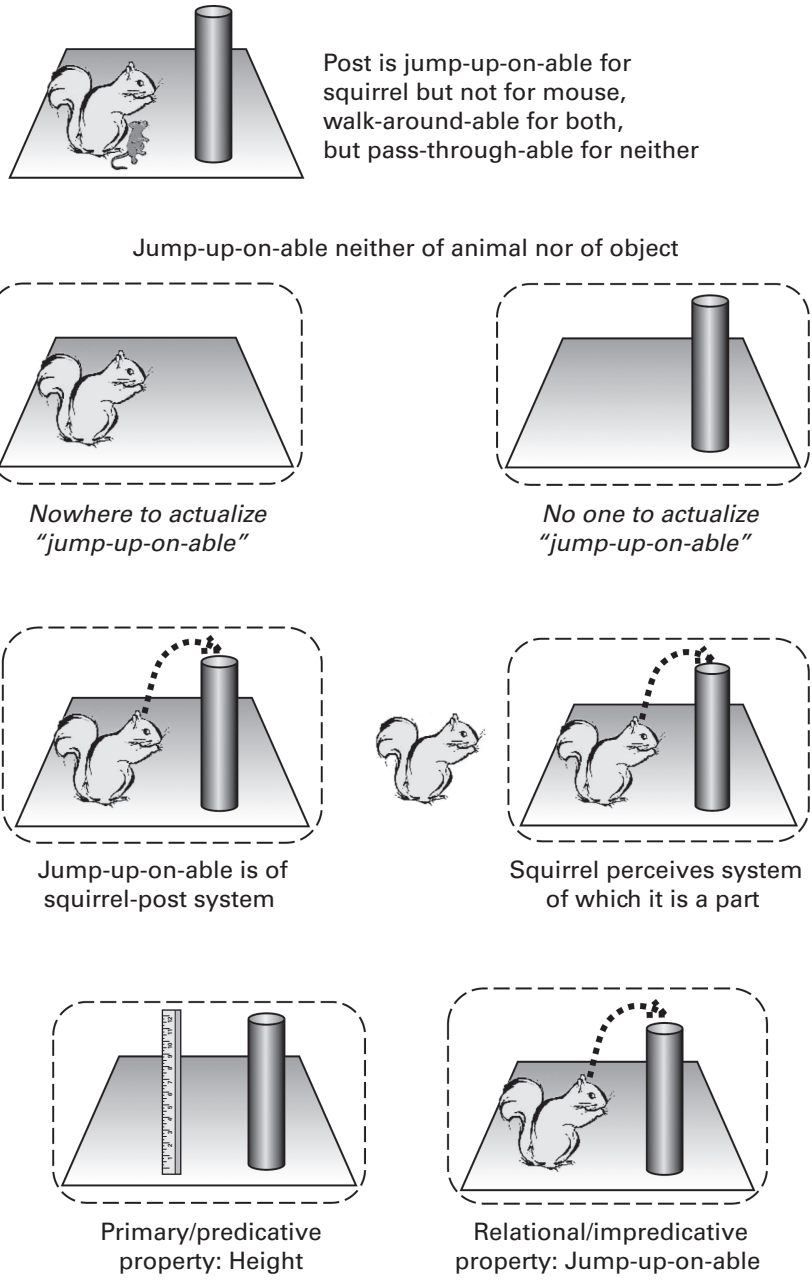


Figure 6.4

The notion of affordance. The objectivity of affordance: relational/impredicative property is defined relative to an object, just like a primary/predicative property. (Adapted from fig. 2 in Petrusz & Turvey, 2010.)

First, an affordance of a surface layout as a relational property is *objective* in the same way that a primary property is objective: it is defined in relation to another object (as further highlighted in fig. 6.3). Second, an affordance of a surface layout is relational in the *quantum compatible* sense. That is, when one relation is actualized, other relations remain potential (the superposition principle). For the post in figure 6.4, when jump-up-on-able is realized by the squirrel, walk-around-able—for both squirrel and mouse—remains potential. Third, an affordance of a surface layout is relational in the *impredicative* sense. It is a property defined in terms of the system of which it is a part. Its definition is circular, context dependent—impredicative (see Chemero & Turvey, 2007).

In sum, affordance is a kind of relational property that (a) exists whether or not it is perceived or realized, (b) cuts across the subjective–objective dichotomy, and (c) is equally a fact of environment and behavior (J. Gibson, 1979/1986). The implication of feature (a) should not go unnoticed: an affordance of a surface layout exists whether or not the other object in the relation exists, meaning that an affordance of a surface layout has *about-ness* or intentionality in Brentano's classical sense (Gomatam, 1999). On this recognition, one might say that intentionality is the mark of the relational.

Back to Concinnity: Model Independence and Symmetries

The generality of concinnity across the Five Kingdoms taxonomy points to the need for a model-independent approach where general principles have primacy over the detailed particulars of individual cases. That is, we need an approach that explores level-independent regularities of self-coordinating phenomena with the goal of optimizing those lawful properties into principles (Golubitsky & Stewart, 2003). The goal is to extract invariants, to discover the symmetries specific to classes of concinnity.

The model-independent approach is reinforced by three principal lessons derived from inquiry into complexity (Goldenfeld & Kadanoff, 1999). Lesson 1: in simple situations, nature produces complex structures; and in complex situations, nature obeys simple laws. Lesson 2: revealing large-scale structure requires a description that is phenomenological and aggregated and directed specifically at the higher level. Lesson 3: a modeling strategy that includes very many processes and parameters obscures (qualitative) understanding.

A simple-model system, the rhythmic synergy of two or more limb segments, helps to make the lessons clear. The ability to synchronize rhythmi-

cally moving components (e.g., limb segments of humans, body segments of the lamprey eel) is fundamental. It is a primary expression of how movements (a) are organized spatiotemporally, (b) resolve issues of efficiency, and (c) satisfy the competing challenges of stability and flexibility (Kelso, 1994). In broad theoretical terms, 1:1 frequency locking in Animalia of two or more limb or trunk segments is archetypal of collective behavior—the organizing of multiple interactions among neural, muscular, metabolic, and mechanical processes under task-specific intentional constraints.

Given the detail, formulating and validating a model-dependent understanding (that is, a quantitative mathematical model of monofrequency rhythmic coordination incorporating physicochemical principles, neurobiological facts, and assumptions about intentionality) is prone to intractability at worst and lesson 3 at best. The alternative approach, abiding the model-independent strategy, is to develop a qualitative dynamical model that incorporates, in broad strokes, the essential features of synchrony between and among the components of a biological movement system (Kelso, 1995).

The important concinnity property of metastability is that a tendency of the components toward dependence (synchrony, integration, cooperation) is complemented by a tendency of the components toward independence (asynchrony, segregation, competition). A concinnity is therefore an organized state, the components of which are always disposed to participate in other concinnities, in other viable organized states (Kelso & Engstrom, 2006; Turvey, 2007). In respect to the colonial bacteria, ameboid cells, and stomata described earlier, each can comprise multiple organizations, befitting conditions. In respect to two or more limb segments, one organization can seamlessly transform into another, as the squirrel negotiates its arboreal surroundings and the gymnast performs her routine.

Absent the necessary fluctuation term, the coordination dynamics of a concinnity or synergy S_i takes the general form $\dot{\zeta} = S(\zeta, c, \delta_1, \ldots \delta_k)$.. In this dynamic system, ζ is the collective variable or order parameter expressing the given system's pattern, c is the control (or primary bifurcation) parameter, and $\delta_i \ldots \delta_k$ are imperfection or detuning parameters. The bifurcation diagram of S, that is, the full complement of changes in the number and/or types (attractors, repellors) of its fixed points, is the product of c and δ_k in combination and at specific values. In short, S is productive or generative. The unfolding of S dynamics through its parameters automatically generates, in a context-dependent manner, a wide variety of quantitatively different and qualitatively distinct functional organizations. And here is where metastability arises: when an imperfection parameter is sufficiently large, attractors and repellors become inexistent. There are no fixed points,

no strictly stable or unstable states, only tendencies or preferences suggested by their "ghosts."

Back to Opportunistic Coupling: Strong Anticipation

The central issue of agency was previewed earlier. Agency's flexibility aspect in the Five Kingdoms has been given due consideration, the complementing features of prospectivity and retrospectivity much less so.

Anticipating Synchronization

Prediction of the future given a model has been termed *weak anticipation*, and prediction of the future not given a model—and relying instead on systemic lawfulness—has been termed *strong anticipation* (Dubois, 2001).

Voss (2000) has identified a general framework for the anticipation of a master system (e.g., light–dark cycle) by a slave system (e.g., organism) with delays:

$$\dot{x} = g(x)$$
$$\dot{y} = f(y) + k(x - y_\tau)$$

The term y_τ identifies a past state of y delayed by τ. The effect of the coupling term $k(x - y_\tau)$ is to minimize the difference between the state of x at the current time and the state of y at a past time. If this difference is successfully minimized, then the difference between the present state of y and the future state of x is also minimized. The effect of this minimization is the synchronization of y with the future of x—strong anticipation (see, e.g., Stepp, Chemero & Turvey, 2011; Stepp & Turvey, 2010).

Proper Organization

The referent perception-action capability for acquiring intuitions about strong anticipation is the outfielder problem. A nonanalytic, non-model-based strategy for solving the outfielder problem common to baseball and cricket identifies the significant optical variable as the vertical optical acceleration of the ball's projection onto the image plane (Oudejans et al., 1996). The outfielder so behaves as to nullify this optical quantity. Catching a fly ball, therefore, is a matter of adjusting one's locomotion to keep the vertical velocity of the ball's projection on the image plane constant. "Getting to the right place at the right time is not solved by prediction, but by continuously adapting the action to information" (Michaels & Zaal, 2002, p. 173).

The outfielder is tied to the ball by the imposition of a relational property. When the *proper organization* of ball and outfielder is in place, the ball

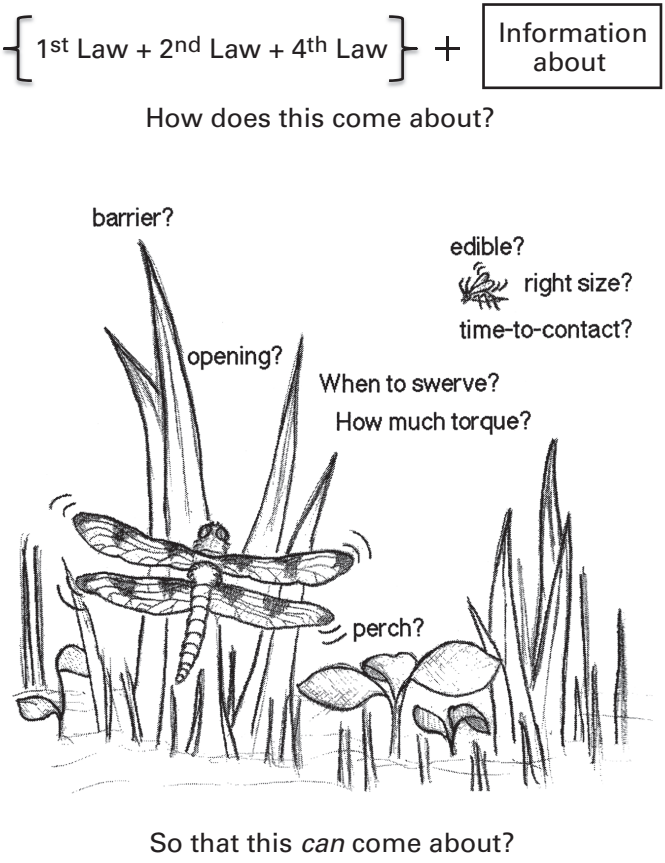


Figure 6.5

A synopsis. The challenge is to understand how ACK systems arise and couple to information (in the specificational sense) through the principles of energy conservation (first law), energy dispersion (second law), and amplification of entropy rate production (fourth law). If the challenge is met, then a first-principles understanding of perception-action capabilities exhibited by members of the Five Kingdoms (such as the dragonflies of Animalia) could follow. (Bottom figure: *The Science of the Mind: 2001 and Beyond* by Robert L. Solso and Dominic W. Massaro [1995], figure 11.3 on p. 155 in "Toward an ecological physics and a physical psychology," by M. T. Turvey and R. E. Shaw, by permission of Oxford University Press.)

and outfielder become a single system with new dynamics. Where and when the fielder intercepts the ball are completely entailed by the *natural unfolding of this new single system*.

The "Unmet Challenge"

By way of conclusion, a suggestion can be made about the "unmet challenge" discussed earlier: on what basis could an ACK system become linked to energy distributions as information about—the sine qua non of prospective control? Anticipatory synchronization might provide such a basis. At issue is whether, given a cyclic regularity of the environment, the coupling relevant to the regularity can be discovered through self-organizing processes. Can ACK dynamics and environmental dynamics, like the outfielder and the ball, become properly organized?

Coda

This chapter has been directed at perception-action writ large, as an inevitable consequence of first principles. Figure 6.5 provides a synopsis. The chapter's content contrasts sharply with standard perspectives on action science. The core concern has been the limits of the science brought to bear on understanding the action manifest by all phyla—what might be termed the science's *problem of impoverished entailment* (Turvey, 2004b). Enriching the entailment requires giving greater emphasis to ontology (rather than epistemology) and the laws that ground organism-environment systems.

Notes

1. It should not be assumed that noninferential accounts are free of such questions. The most famous, advanced by Gestalt psychology, is similarly a three-terms account. The mediator is the principles of brain organization.

2. If not, then perpetual-motion machines would be possible.

3. In the literature (e.g., Kleidon & Lorenz, 2005), one finds other seemingly related designations, most notably maxENT (for "maximum entropy") and MEP (for "maximum entropy production"), a derivative of maxENT. These terms refer to a very different notion, one closer to traditional linear equilibrium thermodynamics and Shannon's entropy, a measure of observer ignorance or uncertainty (rather than a physical quantity). The contrasts between maxENT, MEP, and LMEP, and their motivations, are addressed in Martinez-Kahn and Martinez-Castilla (2010; see also footnote 5 in Swenson, 2010).

4. From *auto* (self) + *cata* (down) + *kinetic* (of the motion of material bodies and the forces and energy associated therewith), from *kinein* (to cause or move).

5. It should be noted that the validity of this claim has been questioned by Wells (2006).

6 There is considerable discussion on the foundational conceptions needed to build a theory of affordances. The literature includes, but is not exhausted by, the following: Chemero (2009), Mace (2005), Michaels & Carello (1981), Reed (1996), Shaw, Turvey & Mace (1982), Shaw (2003), Stoffregen (2003), Turvey (1992).

7 A summary of human affordance research can be found in Richardson, Shockley, Riley, Fajen & Turvey (2008).

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7 Perception Viewed as a Phenotypic Expression

Dennis R. Proffitt and Sally A. Linkenauger

Man [the body] is the measure of all things.
—Protagoras (ca. 490–430 BC)

Introduction

In this chapter, we present and provide empirical support for an embodied approach to visual perception. We propose that visual information is scaled by the perceiver's phenotype in ways that promote effective actions in the immediate environment. Aspects of this approach have been articulated previously (Proffitt, 2006, 2008), but since then, our thinking has evolved considerably as a greater breadth of perceptual phenomena has been investigated. Proffitt (2006) proposed that "what one sees in the world is influenced not only by optical and ocular-motor information, but also by one's purposes, physiological state, and emotions" (110). This statement could be understood as suggesting that visual and nonvisual information are combined in perception, thereby making perception a hybrid, consisting of information of mixed perceptual and nonperceptual origins. We do not ascribe to this hybrid view; instead we argue that visual information is not combined with, but rather *is scaled by*, nonvisual metrics derived from the body. How could it be otherwise? We do not perceive visual angles, retinal disparities, and ocular-motor adjustments, which are the stuff of visual information; rather, we perceive our environment. The angular units of visual information must be transformed into units appropriate for the specification of such parameters of surface layout as extent, size, and orientation. We propose that these scaling units derive from properties of the body in a way that makes perception, like all other biological functions, a phenotypic expression.

This chapter consists of two parts, the first of which provides the conceptual foundations for our account. In essence, we propose that visual

experience relates the optically specified environment to people's ever-changing purposes and the embodied means by which these purposes are achieved. Depending on their purpose, people turn themselves into walkers, throwers, graspers, and so on, and in so doing, they perceive the world in relation to what they have become. People transform their phenotype to achieve ends and scale their perceptions with the aspect of their phenotype that is relevant for their purposive action. The chapter's second part presents empirical support for this embodied approach. The reviewed studies show that (1) within near space, apparent distances are scaled with morphology, and in particular, to the extent of an actor's reach or the size of his or her hand; (2) for large environments, such as fields and hills, spatial layout is scaled by changes in physiology (the bioenergetic costs of walking relative to the bioenergetic resources currently available); and (3) for target-directed actions, behavioral performance scales apparent size; for example, a golf hole looks bigger to golfers when they are putting well. In summary, the evidence shows that perceived spatial layout is scaled by the aspect of the individual's phenotype that is relevant for the execution of purposive action.

Perception Viewed as a Phenotypic Expression

To illustrate the notion of phenotypic expression, consider two individuals, a sumo wrestler and an endurance runner. The sumo wrestler likely has a genetic disposition that made his chosen sport reasonable; moreover, he placed himself in training and eating environments that promoted strength and girth. Similarly, the endurance runner was probably drawn to her sport by a favorable genetic disposition; however, she selected training and eating environments that promoted endurance and a svelte physique. Both individuals chose their sport and developed the requisite phenotypes. By our account, both also perceive the world relative to what they have chosen to become.

The phenotypes expressed by the sumo wrestler and endurance runner entail a dynamic interaction over time between the environments that they have selected, their bodies, and their purposes. As illustrated in figure 7.1A, perception viewed as a phenotypic expression likewise entails an interaction between these three terms, each of which is discussed hereafter.

Environment

Following Gibson (1979), we are drawn to the view that the visually perceived environment is fully specified by visual information. That is, we

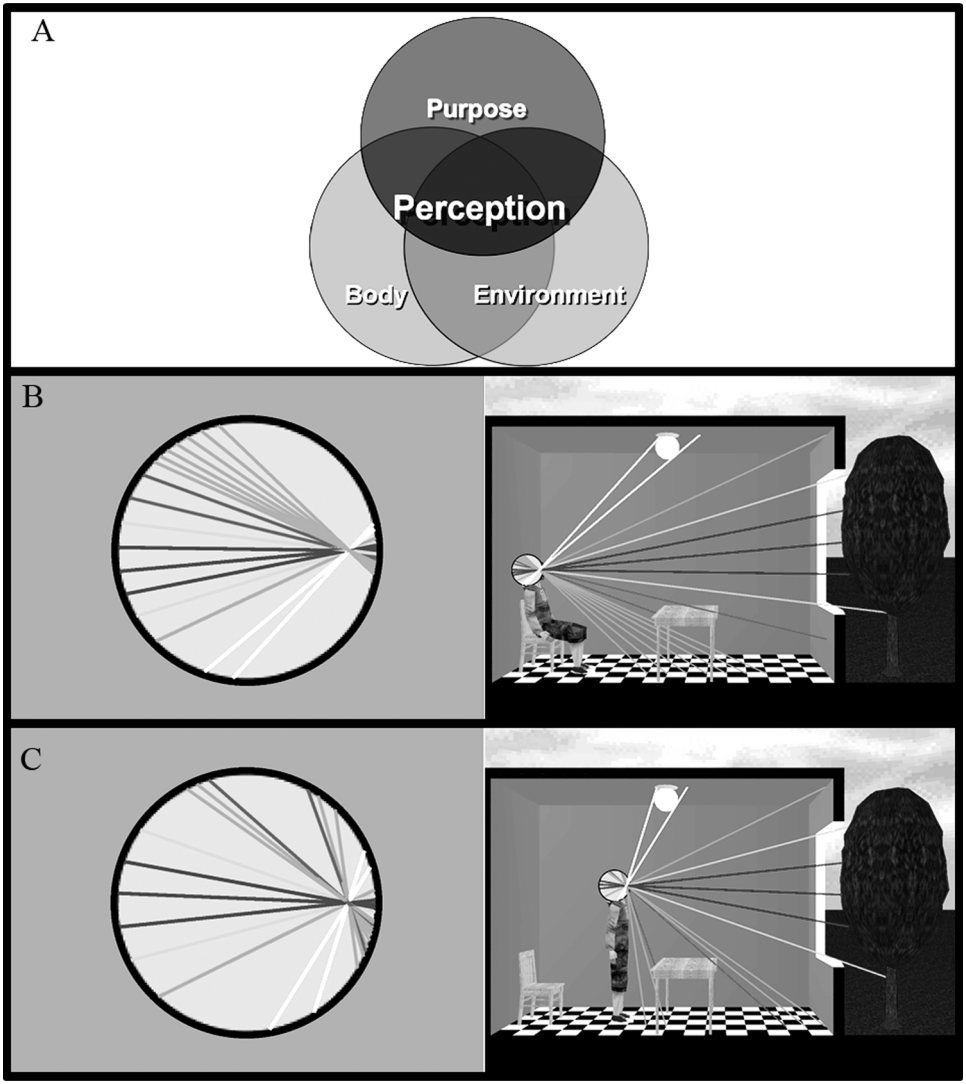

Figure 7.1
(A) Perception expresses the fit between environments, bodies, and purposes. (B) and (C) The visual angles projecting to the eye from an illuminated surrounding.

ascribe to the notion that in a well-illuminated, natural environment, the visual information available to moving observers is sufficient to specify what is perceived; available information does not require augmentation from memory, inferences, or other mediators. Our account, however, does not rest on this predilection. Any account of perception—direct, inferential, or otherwise—must address the problem that the units of manifest visual information are not appropriate for describing the parameters of perceived spatial layout.

The right panels of figure 7.1B–C, adapted from a drawing in Gibson's book (1973, pp. 195), illustrate the situation in which visual perception occurs. The environmental layout surrounding a perceiver consists of surfaces having different locations, shapes, extents, and orientations. The illuminated edges and textures of these surfaces project into the eyes as an indefinite nesting of luminance-defined angles (visual angles), and as the perceiver moves, all these angles change (optic flow). The left panels of figure 7.1B–C illustrate the projection of these angles into the eye. Animations of these figures can be viewed at http://www.faculty.virginia.edu/perlab/misc/bookanimations. Thus the units of visual information consist of angles, these being visual angles, changes in these angles over time, ocular-motor adjustments, and retinal disparities, the latter two of which also scale as angles.

The visual system uses this angular information in two quite different ways. First, it guides actions using visual control heuristics that are applied directly to visual angles, and second, it provides an explicit awareness of the environment by rescaling manifest angular information into dimensionally relevant units.

Visually Guided Actions

Many, perhaps all, visually guided actions are achieved via visual control heuristics that directly relate visual angles to behavior. Consider the oft-studied action of catching a fly ball. In baseball, an outfielder observes a batted ball flying in his general direction and runs to intercept and catch the ball. The control of the fielder's running is guided by visual control heuristics such as the linear optical trajectory (LOT) heuristic (McBeath, Shaffer & Kaiser, 1995). Following this heuristic, fielders run so as to nullify the projected curvature of the ball's trajectory relative to the plane defined by the line of gaze to the ball. If the fielder's running succeeds in causing the ball's trajectory to follow a straight path, then he will intercept the ball. In fact, unless other actions are taken, the ball will hit him in the head. With respect to catching fly balls, other visual control heuristics have

been proposed that additionally entail running to achieve a constant velocity in the ball's projected trajectory (Fink, Foo & Warren, 2009; Oudejans, Michaels &Bakker & Dolné, 1996). To learn more about visual control heuristics, see Fajen (2007) and van der Kamp, Oudejans & Savelsbergh (2003) for excellent reviews.

Visual control heuristics directly couple changes in visual angles to ongoing behavior. Specification of environmental layout is not needed. When catching a fly ball, fielders must run in a manner that produces a linear trajectory in the proximally projected, 2-D motion path of the ball. The location at which they will intercept the ball is not specified. The outfielders do, of course, have explicit awareness of where they are and what they are doing; however, this awareness is not specified by the visual control heuristics that are guiding their behavior.

Explicit Awareness

Outfielders need to watch the ball; "keep your eye on the ball and run" is the principal contribution of explicit awareness to the act of catching. Fielders probably assume that they know where they are going; after all, they are aware that they are running and likely assume that their explicit awareness is somehow in control of their behavior. For the most part, it is not. Even professional baseball players are not good at predicting the locations where fly balls will land (Oudejans et al., 1996).

We propose that, compared to visual control heuristics, explicit awareness is related to action in a less immediate and more deliberate way. In particular, explicit awareness supports decisions about what actions are possible in an environment and the associated costs and benefits of these actions. However, to achieve explicit awareness of the environment's spatial layout, visual information must be rescaled from manifest angles into units appropriate for specifying the dimensions of the environment. We propose that these units derive from the body.

Body

We began this chapter with an epigraph from Protagoras, "Man [the body] is the measure of all things." Applied to perception, this notion must be true. Consider, for example, the world perceived by Gulliver versus the Lilliputians in Jonathan Swift's *Gulliver's Travels* (1726). To Gulliver, the Lilliputians and their artifacts seemed tiny, whereas to the Lilliputians the reverse was true. Each perceived extents and size relative to the size of their own bodies.

Protagoras's insight is consistent with Gibson's (1979) ecological approach to perception, especially his notion of *affordances*. Gibson defined

an affordance as the functional utility of objects and surfaces for an organism having a particular body and behavioral repertoire. For example, a rock affords being picked up if it is of a size that can be grasped. Assuming that it can be grasped, then it can also be dropped, thrown, rolled, kicked, used as a hammer, and an indefinite number of other actions compatible with the actor's morphology and the rock's form, size, and substance. With respect to Gulliver and the Lilliputians, the affordances of a given rock vary greatly depending on the actor. What Gulliver sees as a pebble is a boulder to the Lilliputians.

The growing literature on embodied perception and cognition contains little discussion of what constitutes a body. In biology, a body is described as a phenotype, consisting of three attributes: morphology, physiology, and behavior. Phenotypes vary from species to species; within species there are phenotypic individual differences; and within individuals there are moment-to-moment changes in phenotypic expression.

Morphology

Morphology is the semipermanent form, structure, composition, and size of the body. Morphology places constraints on what organisms are capable of doing; for example, a fish can breathe underwater, but people cannot. Morphology also places constraints on the range of sizes and extents over which actions are possible; for example, the hand's morphology makes grasping possible, but only over a range of object sizes bounded by the maximum extent of an individual's grasp.

Morphology is the physical mechanism through which the dynamic processes of physiology and behavior are realized. In the scaling of visual information, morphology provides perceptual rulers, derived from bodily dimensions such as hand size, arm length, and eye height.

Physiology

Physiology consists of all the metabolic processes that occur in the body over time. Physiological processes, such as blood pressure, stomach acidity, and immune system states, fluctuate as needed to maintain homeostasis, fuel ongoing behavior, and conserve internal resources. Of particular interest to our account are the physiological processes related to energy expenditure and its conservation.

All living organisms are bioenergetic systems with a common imperative to ensure that, over time, energy expenditure does not exceed energy input (Schrödinger, 1945). In accord with this imperative, situations arise in which visual information is scaled by the amount of bioenergetic

resources required to perform an action. This scaling is made possible through learning. Because both physiology and behavior are controlled by neural processes, their covariation can be learned such that a given action over a spatial extent comes to be associated with a specific quantity of bioenergetic cost.

Behavior

Behavior encompasses both an organism's behavioral repertoire and its immediate actions. In the first sense, behavior is an atemporal construct consisting of the activities that, through evolution and development, an organism is capable of performing. The second sense of the term refers to the immediate, ongoing activity in which the organism is engaged. The behavioral repertoire defines a set of roles that an actor can take. Given that actors possess the requisite abilities, they can, at will, turn themselves into "walkers," "throwers," "leapers," "graspers," or an indefinite number of other action-specific phenotypes. As actors move from one role to another, phenotypic reorganizations are required to coordinate current and anticipated performance.

Behavior influences the scaling of spatial perceptions in two ways. First, choosing a role from one's behavioral repertoire determines what aspect of an actor's phenotype is relevant as a perceptual ruler. Being a grasper makes hand size relevant, whereas being a reacher brings arm length into relevance. Second, for target-directed actions, immediate performance can scale the apparent size of the target. As an example to be discussed later, the apparent size of a golf hole is directly correlated with putting success.

Before discussing *purpose*, the final term in our triumvirate of perceptual determinants (fig. 7.1A), we think it best to provide a concrete example of body-based perceptual scaling. To this end, once again we take inspiration from *Gulliver's Travels*.

An Example of Morphological Scaling via Eye Height

Gulliver and the Lilliputians perceive the same world but at proportionally different size scales. Both perceive the world in relation to their body's size. Thus, being bigger, Gulliver sees a smaller world than do the small Lilliputians. So it is with us all. The taller a person, the shorter his or her surroundings are perceived to be.

The top left panel of figure 7.2 shows a man—let's call him Oliver—standing on a path between two rows of pillars of equal height. As Sedgwick (1973) showed, the intersection of the horizon with the pillars provides a ratio of extents specifying that the pillars are all of equal size

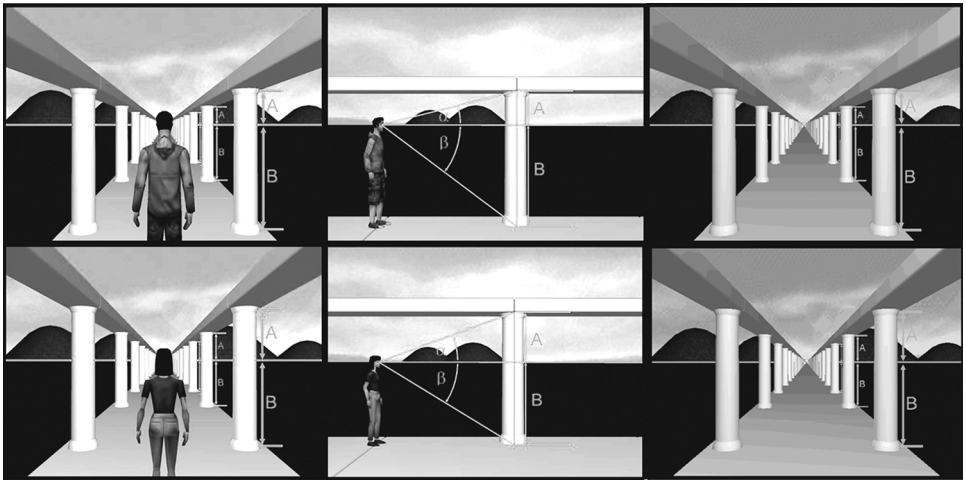

Figure 7.2
The eye-height scaling of size for two people of different height.

regardless of distance and retinal image size. This horizon ratio is defined by the extent from the top of the pillar to the horizon, A, divided by the extent from the bottom of the pillar to the horizon, B. A/B is invariant so long as Oliver and the pillars are on level ground. As shown in the center panels of figure 7.2, the horizon is defined by the line of gaze parallel to the ground plane. Even if not visible, the horizon is robustly specified by a bifurcation in optic flow that occurs at its location. As Oliver walks forward, all the optically specified texture in his surroundings that is above his eye's altitude will move up, and all that is below will move down. The location where the horizon intersects the pillars corresponds to Oliver's eye height, EH, and thus the pillars' size, via the horizon ratio, can be scaled as a proportion of Oliver's eye height. (The pillar height is A + B. B is equal to EH. A/B provides A's extent as a proportion of EH; thus A + B can be expressed as a proportion of EH.)

The bottom panels of figure 7.2 show the same scene viewed by a woman, Lilly, who is shorter than Oliver. Again, the A/B horizon ratio of the pillars is invariant with distance, but notice that the ratio is bigger because Lilly is shorter. As with Oliver, Lilly sees the pillars as having a constant size, but she perceives the pillars as proportionally bigger. The right panels of figure 7.2 show this scene as viewed by Oliver (top panel) and Lilly (bottom panel). Note that the pillars appear proportionally shorter to Oliver than to Lilly. An animation of this scene as viewed by

Oliver and Lilly can be viewed at http://www.faculty.virginia.edu/perlab/misc/bookanimations.

Eye-height scaling of size is an example of how morphology can be used as a perceptual ruler. Perceptual rulers transform visual angles into extent-appropriate units. In eye-height scaling, the specification of extent B by angle β is transformed into a unit of eye height, and the pillar's height is perceived as a proportion of this eye-height metric. More generally, perceptual rulers transform the manifest angles of visual information into proportions of a particular aspect of one's phenotype. To determine which phenotypic component is the appropriate perceptual ruler for the current situation, the notion of purpose must be introduced.

Purpose, Phenotypic Reorganization, and Relevance

Figure 7.3 shows one of us, DP, standing by a stream while hiking in Ireland. At that moment, I was surrounded by an indefinite number of environmental affordances. For example, there were stones on the ground

Figure 7.3
The first author (DP) in surroundings that offer an indefinite number of possibilities for action.

that afforded grasping, a trail that afforded walking, and a stream that afforded crossing, but only by my jumping over it. My purposes determined the affordances I would select and the actions I would perform. Enacting my purposes requires phenotypic reorganization. To pick up the stone, I would become a reacher and grasper; to continue my hike, I would become a walker; and to cross the stream, I would become a jumper. Thus my purposes mandate a goal-directed phenotypic reorganization, which in turn determines what aspect of my body is relevant for scaling my spatial perceptions. As a reacher and grasper, my arm length and hand size would be relevant; as a walker, spatial extents would be scaled by the walking effort required to traverse them; and as a jumper, the extent of my jumping ability would be relevant for measuring the stream's width.

The visually specified environment offers indefinite possibilities for action (Gibson, 1979). Individuals' purposes determine which actions are selected. Moreover, these choices also dictate phenotypic reorganizations to enact the selected behaviors. Returning again to figure 7.3, if my purpose is to throw a stone, then I will visually search the ground for a stone of suitable size. Upon finding a candidate stone, I will become first a reacher, then a grasper, and finally a thrower. Each phenotypic organization determines both what I become and the particular aspect of my body that is relevant for scaling the environment.

Relevance is a key notion in our account. We propose that people scale their spatial perceptions with the aspect of their body that is *relevant* to the situation. For example, when intending to reach, arm length is relevant; however, when intending to walk under a low branch, eye height, not arm length, becomes relevant in deciding whether to duck. The body provides a plethora of perceptual rulers. The ruler employed in any situation is determined by what is relevant given what the actor is attempting to do and the phenotypic organization that has been attained to carry out the intended action. Perceptual rulers transform visual information into units appropriate for size and extent, and in so doing, perceptual rulers provide the units of meaning for our spatial experience. The meaning of an extent is its magnitude on a specific ruler. As seen in the example of Gulliver and the Lilliputians, whether an object is seen as small or large depends on whether Gulliver's or a Lilliputian's perceptual ruler is used for the object's measurement. This body-scaling relationship was recently demonstrated in an aptly titled paper, "Being Barbie: The Size of One's Own Body Determines the Perceived Size of the World," in which participants viewed the environment from the perspective of being in a doll's body or that of a giant (van der Hoort, Guterstam & Ehrsson, 2011). In

addition, for given individuals, perceptual meanings vary from moment to moment as they reorganize their phenotypes to pursue different actions, thereby making different perceptual rulers relevant. In the remainder of this chapter, we elaborate and provide empirical support for this account of perception viewed as a phenotypic expression.

Empirical Support: Phenotypic Scaling of Spatial Layout

Phenotypic scaling of spatial layout uses perceptual rulers derived from morphology, physiology, and behavior. Each is discussed in turn. A fourth section under this heading examines the consequences of phenotypic reorganization in switching perceptual rulers.

Morphology: Action Boundary Scaling

Morphology places constraints both on what actions are possible and on the range over which these actions can be performed. For example, arms allow for reaching, whereas the length and flexibility of individuals' arms define the maximum extent of reach. Maximum reaching extent is an *action boundary*, an exceedingly useful term introduced by Fajen (2005). Action boundaries exist for all the behaviors in one's behavioral repertoire, and they specify the physical limits of successful performance.

To determine whether an action can be performed over a given extent, actors must scale the prevailing visual information to the relevant action boundary. This requires that individuals learn the visual specification of their action boundaries for a great variety of actions. Throughout life, people learn how visual information and their actions are coupled. As Gibson (1979) stated, "Infants, both monkey and human, practice looking at their hands for hours, as well they should, for disturbances of optical structure that specify the niceties of prehension have to be distinguished" (p. 120). During early development, these relationships are likely learned by trial and error. Infants and toddlers have abundant opportunities to learn the visual consequences of their movements. For example, until about six months, infants exhibit the palmer grasp reflex, in which they automatically grasp objects that touch their hands (Twitchell, 1965). Five-month-old infants spontaneously make from 100 to 250 hand movements every 10 minutes when alert (Wallace & Whishaw, 2003). Additionally, a typical toddler traverses roughly 39 football fields a day and falls down about 15 times every hour (Adolph, 2008). Extensive practice allows individuals to learn how their movements are associated with optic flow. Actors learn how to move so as to achieve desired changes in their visually specified

world. Similarly, they learn what visual information is associated with their action boundaries.

An actor's intended action determines the relevant action boundary for scaling spatial layout. For example, if one intends to reach for an object within near space, then the maximum extent of arm's reach becomes the relevant action boundary. For targets within this range, the visual angles specifying extents are scaled as a proportion of that action boundary. Action boundaries function as perceptual rulers, which measure the environment in terms of the body's ability to perform intended actions. Should Gulliver and a Lilliputian both seek a stone to throw, both will find one of a size appropriate for their respective action boundaries for grasping, and in this sense, both will see their selected stone to be roughly equivalent in body-scaled units. However, as measured by an arbitrary metric, such as a metric-scale ruler, the sizes of the two stones would be of very different magnitudes. By scaling spatial layout to morphology, action boundaries specify the fit between people's purposive behavior and the environment.

The magnitude of action boundaries varies across individuals and situations. For example, the action boundary for reaching differs both with individual differences in morphology and also with manipulations altering individuals' reaching extent, for example, the provision of a hand tool. Consider the top panel of figure 7.4. The actor on the right has a longer arm, and consequently a greater action boundary for reaching, than does the actor on the left. Hence, for the actor on the right relative to the one on the left, the perceptual ruler is longer; the depicted circular target measures as a smaller proportion of maximum reach, and as a result, it appears closer. The bottom panel of figure 7.4 depicts the analogous situation for grasping. For people with small hands (Lilliputians), a particular graspable object appears larger than it does to those with bigger hands (Gulliver).

In general, our investigations of phenotypic influences on spatial perceptions have followed two paradigms. First, we have employed experimental manipulations that alter participants' phenotypes in some way, for example, increasing reaching extent through the provision of a hand tool. Second, we have taken advantage of inherent individual phenotypic differences, for example, by relating the variability of perceived extents in near space to the variability in participants' arm length. In the next two sections, we review evidence showing that both within-subject manipulations and individual differences in action capabilities can influence perceived extents in the contexts of reaching and grasping. We also briefly provide supporting evidence from studies on other actions.

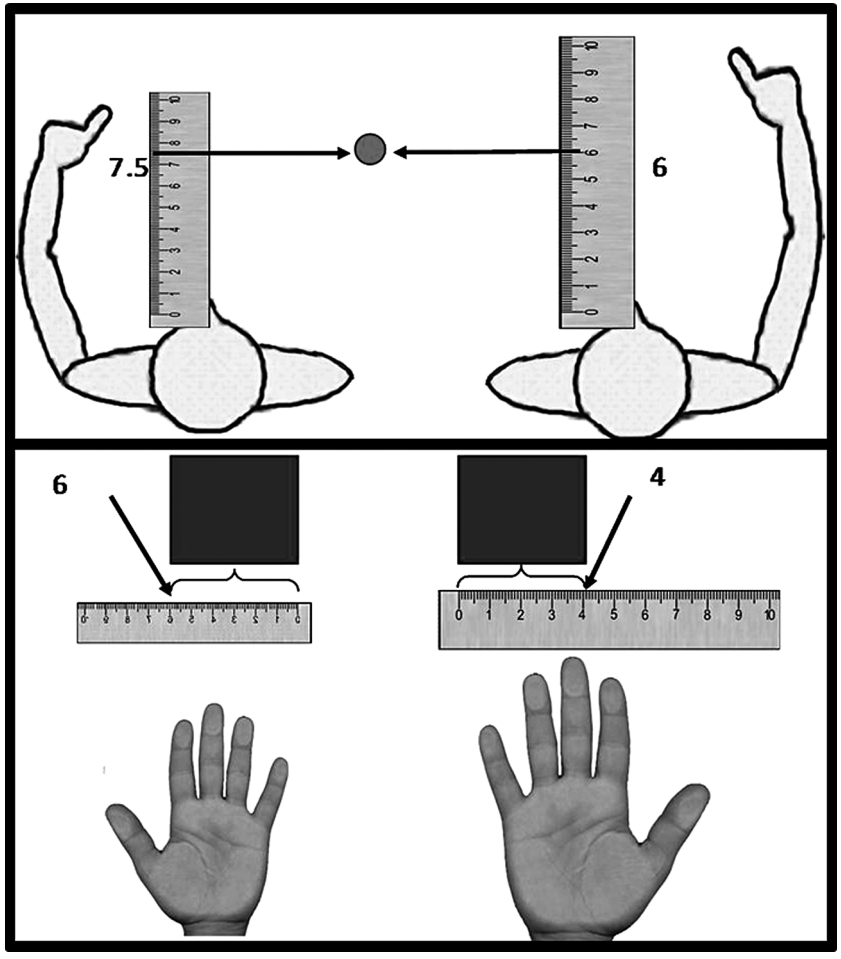

Figure 7.4
An extent in near space can be scaled by the action boundary for reaching (top panel) or grasping (bottom panel).

Reaching

Several studies have shown that manipulating the action boundary for reaching can influence apparent distances to reachable targets. In some studies, participants' reach was augmented by providing them with a hand tool, and it was found that targets, outside arm's reach but within tool's reach, appeared closer when the tool was used for reaching than when it was unavailable (Witt, Proffitt & Epstein, 2005; Witt & Proffitt, 2008). Presumably, when participants reached with the hand tool, their perceptual ruler was expanded, the targets' distances were measured as being shorter, and consequently targets appeared closer. In these experiments, participants used visual matching tasks to estimate apparent distances. Other studies employed manipulations of grasp posture to decrease maximum reaching extent; these manipulations were found to evoke increases in perceived distance by about 5 percent (Linkenauger, Witt, Stefanucci, Bakdash & Proffitt, 2009).

Experimental demand characteristics are always a concern when experimental manipulations are employed, and Loomis and Philbeck (2008) have argued that converging operations using indirect measures of distance can serve as safeguards. Studies employing such indirect dependent measures have found not only that apparent distances to targets are influenced by the use of a tool but also that assessments of perceived shape and parallelism are affected in a manner consistent with the changes found for perceived distances (Witt, 2011).

Individual differences in reaching capabilities have also been shown to influence the perceived distances to reachable targets. Quite amazingly, right-handed individuals perceive their right arm as longer than their left, and consequently they think that they can reach farther with their right hand than with their left (Linkenauger, Witt, Bakdash, Stefanucci & Proffitt, 2009). This asymmetry causes right-handed individuals to perceive distances to be closer when intending to reach with their right as opposed to their left hand (Linkenauger, Witt & Proffitt, in preparation). By the rules of measurement, if an extent (plotted on the abscissa in arbitrary units) is measured by two rulers of unequal unit length (plotted on the ordinate), then the resulting functions will have the same intercepts but different slopes (see fig. 7.4). Consistent with this measurement property, the slope of perceived-to-actual distance when reaching with the right arm was found to be less than the slope of perceived-to-actual distance when reaching with the left, and there was no difference in the intercept between the two functions. An additional study showed that people with longer arms see targets as appearing closer, but only for distances that are within

the individual's arm's reach (Linkenauger et al., in preparation). Distances outside of reach were outside of its action boundary and hence were not influenced by reaching ability.

Other studies have shown that targets within reach are bisected differently than those outside of reach, suggesting that objects within and outside of reach are being scaled differently. For example, when bisecting lines in near space, individuals tend to demonstrate leftward biases, whereas outside of reachable space, individuals tend to demonstrate rightward biases (Varnava, McCarthy & Beaumont, 2002). If individuals' reaches are constricted by wrist weights, the transition between the leftward and rightward bias begins closer to the torso than if they are not wearing wrist weights or, as a control for demand characteristics, if they are wearing a backpack (Lourenco & Longo, 2009). Similarly, for individuals with longer arms, the rightward shift occurs farther from the individual than for those with shorter arms (Longo & Lourenco, 2007). Several patients with hemispatial neglect—a neurological disorder resulting in a lack of awareness for one visual hemisphere—exhibit neglect in either near or far space, but not both (Cowey, Small & Ellis, 1994; Halligan & Marshall, 1991; Keller, Schindler, Kerkhoff, von Rosen & Golz, 2005; Shelton, Bowers & Heilman, 1990; Vuilleumier, Valenza, Mayer, Reverdin & Landis, 2004). Additionally, providing a tool to patients with near-space neglect extends their neglect region (Berti & Frassinetti, 2000).

Grasping

The action boundary for grasping has also been shown to act as a perceptual ruler to scale the apparent sizes of graspable objects. As depicted in the lower panel in figure 7.4, the body-scaled size of a graspable object depends on the size of the hand. As with reaching, manipulations of the hand's perceived size or grasping ability influence the perceived sizes of graspable objects (Haggard & Jundi, 2009; Linkenauger, Ramenzoni & Proffitt, 2010; Linkenauger, Witt & Proffitt, 2011). For example, when the apparent size of the hand is increased by placing the hand in a box that magnifies it, individuals perceive graspable objects to be smaller than when their hand is not magnified (Linkenauger et al., 2011). In these studies, perceived size was assessed by visual matching tasks.

Studies exploiting individual differences have found that people with larger hands perceive graspable objects as smaller than do people with smaller hands (Linkenauger et al., 2011). In addition, right-handed individuals perceive their right hand as being about 7 percent larger than their left (Linkenauger, Witt, Bakdash, Stefanucci & Proffitt, 2009), and

consequently right-handed individuals, when intending to grasp an object with their right as opposed to their left hand, perceive the graspable object as being smaller (Linkenauger et al., 2011).

In addition to reaching and grasping, other action boundaries have been shown to be used as perceptual scales. Jumping ability influences the perceived extent of jumpable gaps (Lessard, Linkenauger & Proffitt, 2009). Throwing ability influences the perceived extent over which one anticipates throwing (Witt, Proffitt & Epstein, 2004). The ability to pass through an aperture affects its perceived size (Stefanucci & Geuss, 2009). The ability to balance on a thin beam of wood influences the beam's perceived width (Geuss & Stefanucci, 2010). The ability to duck under a horizontal barrier influences the barrier's perceived height (Stefanucci & Geuss, 2010).

In summary, a considerable body of research shows that the morphology of relevance for an intended action is used to scale extents within its action boundary. Action boundaries serve both to specify whether an action can be performed and to proportionally scale extents within its range. We now turn to scaling via physiology.

Physiology: Bioenergetic Scaling

For long extents on the ground, the most relevant activity is walking, and for a walker, the unit of measurement is the *amount of walking* required to traverse the extent. It would make little sense, for example, to scale a football field's extent in units of morphology, such as hand size or arm length. We propose that amount of walking is scaled by the bioenergetic costs associated with walking an extent relative to the available bioenergetic resources. In essence, we are proposing a mechanism analogous to measuring extended spatial layout with one's "metabolic gas gauge." We have looked at two aspects of the ground plane relevant for walking, geographical slant and egocentric distance. Much of our past research was previously reviewed in Proffitt (2006, 2008), and thus the following discussion emphasizes more recent research.

Walking on Hills

Initial studies of geographic slant perception entailed manipulations that increased the bioenergetic costs of walking, either by having participants wear a heavy backpack (Bhalla & Proffitt, 1999) or by pulling participants backward with a tether as they walked on a treadmill in a virtual environment (Creem-Regehr, Gooch, Sahm & Thompson, 2004). Other studies decreased available bioenergetic resources by inducing fatigue via exercise (Bhalla & Proffitt, 1999; Proffitt, Bhalla, Gossweiler & Midgett, 1995). Explicit perceptions of slant were assessed by both verbal reports and visual

matching tasks. These studies found that participants judged hills to be steeper as the bioenergetic costs of walking increased or as the available resources decreased.

The backpack manipulation was called into question by Durgin et al. (2009). These authors designed an experiment to show that the influence of the backpack on apparent slant was due to demand characteristics of the experimental situation, not bioenergetic influences. I (DP) had previously raised this possibility: "A very reasonable objection would be that these manipulations might have created a response bias, so that the results might not reflect an influence on perception itself. After all, if people are asked to wear a heavy backpack while making distance judgments, they might well suspect that the backpack is supposed to have an effect on their judgments—why else are they being asked to wear one?" (Proffitt, 2006, p. 115). We can conclude little from the Durgin et al. study, because their experimental paradigm did not generalize to the situation of interest, *walking on hills* (Proffitt, 2009). Durgin et al. employed a two-meter-long ramp that abutted a closed door. Because this small incline did not afford walking, walking effort was irrelevant to scaling its slant. Hence whether the backpack induces demand characteristics in the context of walking on hills remains an open question.

One way to eliminate the possibility of demand characteristics is to study individual differences in bioenergetic potential. These designs employ no experimental manipulations; everyone is treated the same. Such studies have shown that apparent hill steepness increases with reduced physical fitness, increased age, and declining health (Bhalla & Proffitt, 1999).

A recent set of studies, which employed both experimental manipulations and individual differences analyses, looked directly at one of the underlying physiological mechanisms of bioenergetics, blood glucose (Schnall, Zadra & Proffitt, 2010). We found that consuming a glucose-sweetened drink caused participants to see hills as less steep compared to participants who consumed a noncaloric drink. Independent of the glucose manipulation, we also found that individual differences in bioenergetic potential predicted variability in slant perceptions. Individual differences were assessed with a bioenergetic test battery, which assessed levels of fatigue, sleep quality, fitness, mood, and stress. Factors associated with diminished bioenergetic resources were directly related to perceptions of increased geographic slant.

Walking Extents

Egocentric distances on the ground have also been shown to be influenced by manipulations of bioenergetics. Extents appear greater under the following

conditions: wearing a heavy backpack versus not (Proffitt, Stefanucci, Banton & Epstein 2003), throwing heavy versus light balls (Witt et al., 2004), and viewing extents on steep versus shallow hills (Stefanucci, Proffitt, Banton & Epstein, 2005). Woods, Philbeck, and Danoff (2009) failed to replicate the first two findings. We do not know why. By either Durgin et al.'s (2009) demand characteristic account or our bioenergetic account, wearing a heavy backpack should have affected participants' distance judgments. We discuss what to make of such null findings in the conclusion to this chapter.

A far more robust effect of walking effort on perceived distance can be obtained by having people walk on a treadmill, which pairs minimal optic flow with forward walking effort. This pairing induces a perceptual-motor adaptation in which the perceptual-motor system "learns" that it takes forward walking effort to remain stationary (Anstis, 1995; Durgin & Pelah, 1999). Following this recalibration, the perceptual-motor system also learns that more effort is required to walk a prescribed distance than was the case before the treadmill walking adaptation. Consistent with this change in anticipated walking effort, extents appeared substantially greater following treadmill walking adaptation than they did before this perceptual-motor recalibration (Proffitt et al., 2003). In these studies, apparent distances were assessed by verbal reports or by having participants view targets and then walk to their location blindfolded.

A recent double-blind study, employing both an experimental manipulation and an individual differences design, found perceived distance to be strongly influenced by physiological variables (Zadra, Schnall, Weltman & Proffitt, 2010). Competitive bicycle racers participated in two sessions, one in which they received a calorically sweetened drink, and another in which the drink contained a noncaloric sweetener. In each session, participants made pretest distance judgments, ingested one of the drinks, rode a stationary bike at high effort for 45 minutes (during which time continuous measures of heart rate, blood glucose, blood lactate, oxygen uptake and carbon dioxide respiration, and power applied to the bicycle pedals were obtained), and made posttest distance judgments. Those who ingested the noncaloric sweetener perceived distances as greater in the posttest than in pretest, whereas participants who consumed the caloric sweetener actually perceived distances as greater in the pretest than in the posttest. By far, the most compelling evidence for physiological scaling was obtained by looking at individual difference measures. It was found that, independent of condition, posttest distance judgments increased with the following physiological variables obtained during the riding exercise: (1) average

heart rate (inversely related to aerobic fitness), (2) lower levels of blood glucose, (3) higher levels of blood lactate (inversely related to aerobic fitness), (4) calories consumed per minute (derived from oxygen uptake and carbon dioxide respiration), and (5) average power exerted in pedaling. Hence distance perception was influenced not only by manipulating glucose levels but also by individual differences in fitness and energy output.

Behavior: Performance

For several target-directed actions, such as putting in golf, successful performance relies on the performer's skill. Skill is best defined as consistency in the successful performance of a behavior, and this can be quantified by the probability distribution associated with the behavior's execution. Consider figure 7.5A, which depicts the left/right distribution of putts around a hole for two golfers. Neither golfer exhibits an error in mean performance; their mean putting direction is centered on the hole. These golfers do, however, differ in the variability of their error; the putting distribution is more compact for Golfer 2 than Golfer 1. Golfer 2 putts consistently closer to the hole than Golfer 1. The variance of probability distributions can act as a scaling metric for the apparent sizes of goal-directed targets. If perceived target size is scaled by the variance of performance, then Golfer 2 would see the golf hole as larger than Golfer 1, because the golf hole measures as larger on the more compact distribution.

Several studies have shown that individuals scale targets' apparent sizes to their ability to successfully perform target-directed actions. Golfers who were putting better perceived the golf hole as larger, and softball players who had better batting averages for a just completed game saw the softball as larger (Linkenauger & Proffitt, in preparation; Witt, Linkenauger, Bakdash & Proffitt, 2008; Witt & Proffitt, 2005). Individuals who are better at throwing balls or darts to targets perceive the target as larger (Cañal-Bruland & van der Kamp, 2009; Cañal-Bruland, Pijpers & Oudejans, 2010; Wesp, Cichello, Gracia & Davis, 2004). Field goal kickers who are kicking better perceive the distance between the uprights as larger (Witt & Dorsch, 2009). Similarly, golfers perceived the golf hole as larger when their apparent performance variability error was manipulated by projecting a Müller-Lyer illusion–inducing configuration around the golf hole to make individuals perceive that they were putting closer to the golf hole than they actually were (Linkenauger & Proffitt, in preparation; see fig. 7.5B). Perceived size in these studies was assessed via visual matching tasks. Performance can also be affected by perception. When studies used the Ebbinghaus illusion

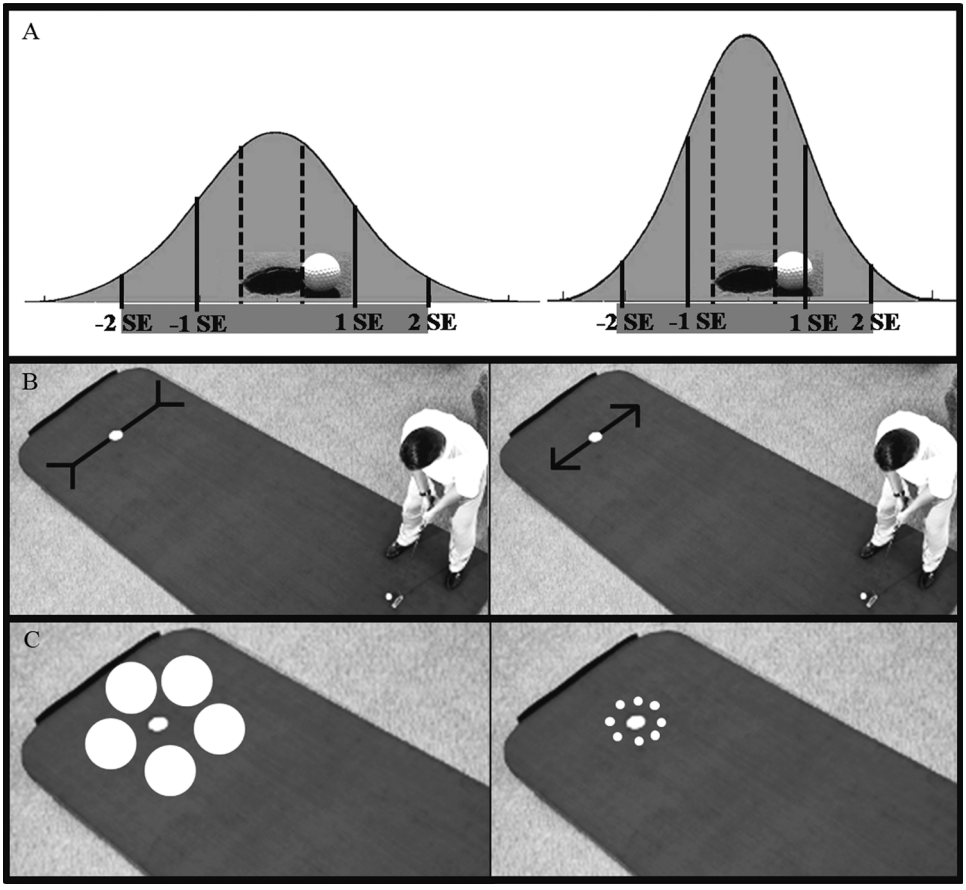

Figure 7.5
(A) The distribution of putts to the left and right of the target hole. (B) An illusory manipulation that influences putters' impressions of the variability of their putting. (C) An illusory manipulation that influences (1) the apparent size of the putting hole and (2) putting performance.

to make the golf hole appear larger, golfers putted better (Witt, Linkenauger & Proffitt, 2012; see fig. 7.5C).

Phenotypic Reorganization

In this section, we discuss what happens when people assume different phenotypic organizations, in particular, when people view their environment as either walkers or throwers.

Phenotypic-Specific Scaling

We have proposed that people scale spatial layout with the aspect of their body that is relevant for their intended action; this is what we mean by phenotypic-specific scaling. To test this notion, we conducted a study in which walking effort was recalibrated by having participants walk on a treadmill for a couple of minutes in the absence of translational optic flow (Witt, Proffitt & Epstein, 2004). Following this adaptation, half of the participants verbally judged the distance to a target under the assumption that they would next walk blindfolded to its location. The second group of participants made distance judgments assuming that they would next throw a beanbag to the target's location. An increase in apparent distance—posttest minus pretest—was found only for the group that anticipated walking the target distance. Because treadmill walking did not influence the effort entailed in throwing, throwers were unaffected in their distance judgments by the recalibration in their walking effort. This study showed that apparent distances are scaled by the aspect of the body that is relevant for intended action.

Changing Phenotypes

In this final study (Witt, Proffitt & Epstein, 2010), we replicated the design of the study presented in the previous section, but with an interesting twist. Again, two groups of participants walked on a treadmill for a couple of minutes and then viewed a target. Unlike the previous study, no verbal distance judgments were obtained. Instead participants were told that after viewing the target they would be blindfolded and, depending on their group assignment, would either walk or throw a beanbag to its location. These instructions were carried out for walkers, but after putting the blindfold on the throwers, the experimenter told these participants, "Oops, I've made a mistake. Actually I would like you to walk to the target." Thus both groups blind-walked an extent that they had perceived with different phenotypic organizations; one group viewed the extent as walkers, the other as throwers. For only the group that had viewed the target as walkers was

blind walking influenced by the treadmill-walking adaptation; consequently they walked a greater distance than did those who viewed the target as throwers. The throwers were unaffected by the treadmill-walking experience because during perception, they viewed the target as throwers, not walkers. A control study was conducted with an identical design except that the treadmill-walking adaptation was eliminated. As expected, there was no difference in the distance walked for walkers and throwers. These studies show not only that perceptions are action specific but also that phenotypic scaling occurs during perception and not during the response process.

Conclusion

Our account is quite simple. We propose that spatial perception relates the environment to our body and to our purposes. In a given situation, we perceive the possibilities for action, and given our purposes, the world is scaled to the aspect of our body that is relevant for the pursuit of achievable aims. The environment is specified by angular information: changing visual angles, ocular-motor adjustments, and retinal disparities. To perceive spatial layout, we need to transform these angles into units appropriate for size and extent. These units derive from the body. Given their current purposes, individuals organize their phenotypes to pursue their aims and, in so doing, transform themselves into action-specific phenotypes, such as graspers, reachers, walkers, throwers, batters, and any of the indefinite number of other phenotypic organizations that we can achieve. Purpose determines our phenotypic organization, which in turn determines the aspect of the body that is appropriate for use as a perceptual ruler. For graspers, hand size is relevant; for reachers, arm length is relevant; and so forth. In essence, our purposes determine what we become—our phenotypic organization—and what we become determines the relevant units of meaning for our spatial experience.

Is our account complete? Of course not. We have painted our approach with broad strokes, and most of the important questions pertaining to spatial perception remain unaddressed. For example, we have few insights into how people scale extents of such vastness that body size is a poor ruler. From my (DP) neighborhood in Virginia, I have a view of the Blue Ridge Mountains, approximately twenty kilometers away. I do have a perception of this extent—though it is extremely imprecise—and I cannot imagine in what units it is cast. What about the perceived size of the Grand Canyon or the moon? Our account is not very helpful in suggesting scaling units for such cases.

Is our account right? For this question, our answer is yes and no. Our central claim must be true; in many situations, the body has to provide the fundamental scales for perceiving size and extent. The example of the differently scaled perceptual worlds of Gulliver and the Lilliputians makes this point obvious, and it is difficult to imagine how it could be otherwise. Do we have all the details right? Of course not. We are happy to be shown where we are wrong so long as better alternative accounts are also advanced. Without the provision of alternatives, null findings provide few insights. For example, a recent study showed that staircases and escalators are perceived to have similar slants though escalators require less energy for ascent (Shaffer & Flint, 2011). The authors contend that this null finding is evidence against our account that effort influences slant perception. This conclusion begs the question of how staircases and escalators are perceptually scaled: if not via the metabolic costs associated with their ascent, then how? Since both staircases and escalators are types of steps, then they could be scaled with morphology and, in particular, the ratio of riser height to leg length (Warren, 1984). The key issue for us is not whether specific predictions based on our account are right or wrong; of course, much of what we have suggested may be wrong. Rather, for us, the key issue is determining how spatial perceptions are scaled. Gibson (1979) often reminded his readers that we do not perceive information; we perceive the world. Visual information must be transformed from angles into extent-specifying units. If these units do not derive from the body, then what is their source?

In summary, we propose that the world is perceived with scales that derive from our body and are appropriate to our purposes. Given the opportunities afforded by our current situation, our purposes determine the actions we pursue and the phenotypic organizations required for their enactment. Our action-specific phenotypic organization determines the aspect of our body that is relevant for scaling the optically specified environment. Through perception, we perceive how our purposes, body, and environment fit together.

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III Neurocognitive Mechanisms

8 Understanding Action from the Inside

Giacomo Rizzolatti and Corrado Sinigaglia

Introduction

Humans are social creatures whose life is characterized by complex interchanges. A striking feature of these interchanges is that others' motor behavior is usually interpreted as a mark of something as insubstantial as mental activity. Actions of others are manifest clues to their goals and intentions just waiting to be captured.

Philosophers, psychologists, and cognitive neuroscientists typically claim that the capability to understand the goals and intentions of others is based on the observers' capability to infer others' internal mental states and to ascribe to them a causal role in generating the observed behavior (Carruthers & Smith, 1996; Malle, Moses & Baldwin, 2001). In our daily life, however, we often make sense of others without resorting to inferential processes, relying instead on an immediate and direct understanding of what others do and why they are doing it.

Neurobiological evidence for a direct understanding of others has been provided by the discovery, in the monkey premotor cortex, of a specific class of neurons discharging both when people perform a given motor act and when they observe someone else performing a similar motor act (di Pellegrino et al., 1992; Gallese, Fadiga, Fogassi & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese & Fogassi, 1996). These neurons are called mirror neurons. Subsequently, researchers have also found mirror neurons in the parietal cortex of the monkey (Fogassi et al., 2005), in motor and viscero-motor human brain areas (see Rizzolatti, Fogassi & Gallese, 2001; Rizzolatti & Fabbri-Destro, 2008), and in song-producing motor areas of birds (Prather, Peters, Nowicki & Mooney, 2008; Keller & Hahnloser, 2009). All these neurons have in common a basic mechanism (the mirror mechanism) that transforms sensory representations of actions into a motor format. According to its anatomical location, this mechanism subserves different functions,

ranging from the recognition of song of conspecifics in birds to action understanding and empathy in humans.

Unfortunately, the limited space of this chapter does not allow us to review the large literature that exists on different functions mediated by the mirror mechanism. We therefore focus on one function: understanding actions done by others. We first provide a picture of the anatomy of the parieto-frontal network in nonhuman primates and humans. We then investigate the functional properties of the neural circuits located within the parieto-frontal network endowed with the mirror mechanism (mirror circuits). We conclude by presenting recent data that suggest that the motor encoding of actions is critical for perceiving the motor acts of others, not only in terms of their goals but also in terms of their specific visual aspects.

The Anatomical Organization of the Parieto-frontal Circuits

Parieto-frontal Circuits in Monkeys

The agranular frontal cortex of the macaque monkey consists of a mosaic of distinct areas (fig. 8.1). The most caudal area (area F1) corresponds to the classical primary motor cortex. The others areas (often referred to as *premotor* areas) can be grouped into two major groups: a caudal one (areas F2, F3, F4, F5p, and F5c) and a rostral one (areas F5a, F6, and F7) (Rizzolatti & Luppino, 2001; Borra et al., 2008). The areas of the caudal group send connections to the spinal cord (He, Dum & Strick, 1993, 1995) and are linked with one another and with F1. The areas of the rostral group control movements indirectly via the brain stem, are not connected with F1, and have widespread connections with the premotor areas of the caudal group.

Cortical input to the frontal motor areas arrives from three main regions: the parietal cortex, the prefrontal lobe, and the rostral cingulate cortex (see Rizzolatti & Luppino, 2001). Caudal premotor areas, as well as area F1, receive their cortical input mostly from the parietal lobe, while the rostral premotor areas receive it mostly from the prefrontal and cingulate cortices.

As the premotor cortex, the monkey's posterior parietal lobe also contains a mosaic of independent areas (fig. 8.1; see plate 1). These areas deal with specific aspects of sensory information and control specific effectors (Rizzolatti, Luppino & Matelli, 1998; Rozzi et al., 2006). Premotor and parietal areas are connected with one another in a highly specific way. Thus, within the global parieto-frontal network, it is possible to identify

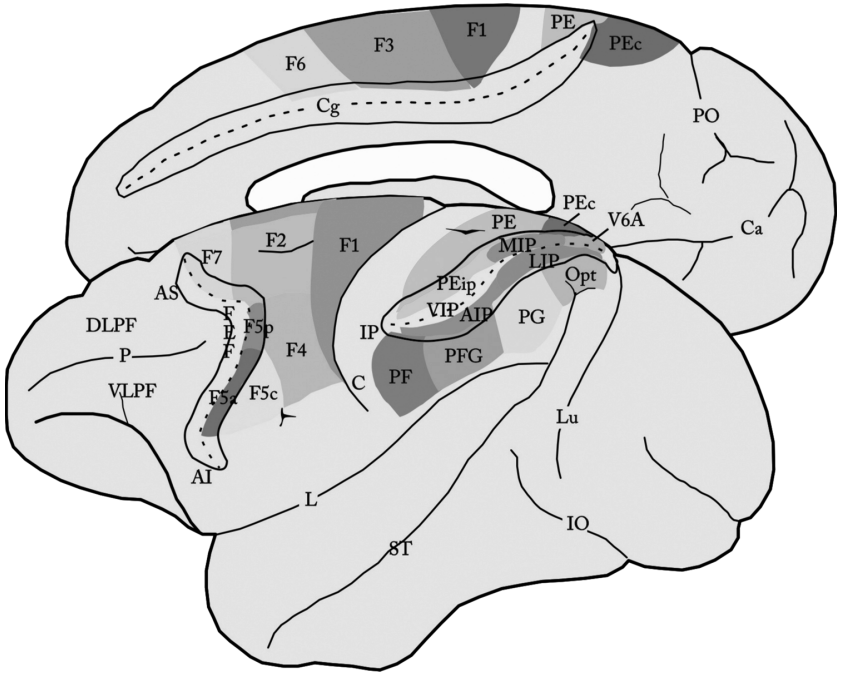

Figure 8.1
Mesial and lateral views of the macaque brain showing the cytoarchitectonic parcellation of the frontal motor cortex (areas indicated with *F* and Arabic numbers) and the parietal lobe (areas indicated with *P* and letters). Areas buried within the intraparietal sulcus (IP) are shown in an unfolded view of the sulcus. AIP, anterior intraparietal area; AS, superior arcuate sulcus; AI, inferior arcuate sulcus; C, central sulcus; Ca, calcarine fissure; Cg, cingulate cortex; DLPF, dorsolateral prefrontal cortex; VLPF, ventrolateral prefrontal cortex; FEF, frontal eye field; F5a, anterior sector; F5c, convexity sector; F5p, posterior sector; IP, intraparietal sulcus; L, lateral sulcus; LIP, lateral intraparietal area; MIP, medial intraparietal area; Lu, lunate sulcus; Opt, occipito-parieto-temporal area; P, principal sulcus; POs, parieto-occipital sulcus; STS, superior temporal sulcus; VLPF, ventrolateral prefrontal cortex; V6a, anterior area V6. (See plate 1.)

a series of largely segregated anatomical circuits formed by parietal and premotor motor areas linked one to another (Rizzolatti & Luppino, 2001).

Parieto-frontal Circuits in Humans

The basic organization of the agranular frontal cortex in humans is similar to that of the monkey (von Bonin & Bailey, 1947; Bailey & von Bonin, 1951). Recent neuroimaging data (Toni et al., 2001; Amiez, Kostopoulos, Champod & Petrides, 2006) and connection studies confirmed this view (Tomassini et al., 2007; Schubotz et al., 2010). As in the monkey, the human mesial premotor cortex consists of two major subdivisions: areas SMA (corresponding to monkey area F3) and pre-SMA (corresponding to monkey area F6) (see Zilles, Palomero-Gallagher & Schleicher, 2004). The human lateral premotor cortex is formed by two main regions: the dorsal (PMd) and the ventral (PMv) premotor cortex. PMd corresponds to monkey F2 and F7, while PMv is formed by monkey F4 and F5.

Unlike in monkeys, where the spur of the arcuate sulcus indicates the approximate border between PMd and PMv (see fig. 8.1 [plate 1]), such a marker is absent in humans. Thus the border between these two regions is difficult to draw. On the basis of embryological considerations, Rizzolatti and colleagues (Rizzolatti & Arbib, 1998; Rizzolatti, Fogassi & Gallese, 2002; Rizzolatti & Craighero, 2004) suggested that the monkey's superior limb of the arcuate sulcus plus the arcuate spur corresponds to the human superior frontal sulcus plus the superior precentral sulcus. Accordingly, they proposed that the border between human PMd and PMv should lie approximately at z level 50 in Talairach coordinates. Recent diffusion tractography data confirmed this location, placing it in different subjects between z level 42 and 56 (Tomassini et al., 2007). Evidence also suggests that in humans PMd and PMv are formed by different areas (Zilles et al., 2004). Their functional equivalence with the monkeys' various premotor areas, however, is not clear (see discussion in Schubotz et al., 2010).

As in other primates, the human posterior parietal lobe (PPL) is formed by two lobules—SPL and IPL—separated by the intraparietal sulcus. Homologies between cytoarchitectonic areas of different species are not easy to draw. Thus it was suggested in the past that IPL in the monkey might correspond to SPL in humans, with human IPL being an evolutionarily new region (Brodmann, 1909). Whereas there is no doubt that IPL dramatically increased in humans and that some functional areas that are present in humans are absent in monkeys (e.g., "action tool" specific area in IPL; Peeters et al., 2009), overwhelming evidence indicates that the basic organization is similar in the two species (for discussion, see Rizzolatti & Matelli, 2003).

Grasping Goals within the Motor System

The Basic Properties of Mirror Neurons in Monkeys and Humans

Early experiments on area F5 of the monkey suggested that neurons in this area code mostly *motor acts* (i.e., movements with a specific goal, such as grasping, ripping, placing), rather than single *movements* (i.e., bodily part displacements devoid of any goal, such as finger flexion) (Rizzolatti et al., 1988; Rizzolatti et al., 2001). Crucial evidence in favor of this view has recently been provided by a study of Umiltà et al. (2008). They recorded single neurons in monkeys trained to use two types of pliers to grasp objects: "normal pliers" and "reverse pliers." To grasp an object, the normal pliers require a closing movement of the hand; in contrast the reverse pliers require a hand opening, that is, a movement opposite to that required by the normal pliers. The results showed that regardless of the pliers used, neurons in F5 discharged during the phase in which an object was grasped; that is, what counted was the goal of the motor act and not the movements that allowed one to achieve that goal.

Some F5 motor neurons respond to visual stimuli. These visuomotor neurons fall into two classes: canonical neurons and mirror neurons. As all other F5 neurons, canonical and mirror neurons encode motor goals, not movements. Canonical neurons discharge in response to the visual presentation of objects. The majority of them respond selectively to objects of a certain size, shape, and orientation (Rizzolatti et al., 1988; Jeannerod, Arbib, Rizzolatti & Sakata, 1995; Sakata, Taira, Murata & Mine, 1995; Murata et al., 1997; Raos, Umiltà, Fogassi & Gallese, 2006; Umiltà, Brochier, Spinks & Lemon, 2007). Typically congruence holds between the motor act that a canonical neuron encodes (e.g., precision grip) and the physical characteristics of the object that activates it (e.g., a raisin).

Unlike canonical neurons, mirror neurons (about 20 percent of F5 neurons) do not fire in response to simple object presentation but require, to be triggered, the observation of a target-directed motor act. The observation of intransitive acts, including mimed actions, is poorly effective or ineffective at all in F5 (Gallese et al., 1996; Rizzolatti, Fadiga, Gallese & Fogassi, 1996). Most mirror neurons show a close relationship between the motor acts they encode and the visual motor acts they respond to. For some neurons, the observed and executed effective motor acts are identical in terms of goal and the way in which that goal is achieved, while for others only the goal is the same in the observed and executed effective motor acts.

The study of the motor properties of neurons of the parietal areas PFG and AIP showed a close similarity with those of area F5, both of them

encoding the goal of the motor acts rather than individual movements (Rozzi et al., 2006). Similarly, the visual properties of many PFG and AIP neurons are akin to those of F5 neurons. In particular, some PFG and AIP neurons are endowed with mirror properties and respond to the motor goal of the observed action. The percentage of mirror neurons in PFG relative to all visual responsive neurons is about 15 percent (Rozzi et al., 2006). No quantitative data are available for AIP.

Several early brain-imaging studies suggested that human "mirror" areas encode the goal of the observed motor act (Rizzolatti, Fadiga, Matelli, Bettinardi, Paulesu, Perani & Fazio 1996; Grafton, Arbib, Fadiga & Rizzolatti, 1996; Buccino et al., 2001; Decety, Chaminade, Grèzes & Meltzoff, 2002) (see fig. 8.2 [plate 2]). Strong recent support for this view came from two series of experiments. First, these studies demonstrated that the parieto-frontal areas endowed with mirror properties become active during the

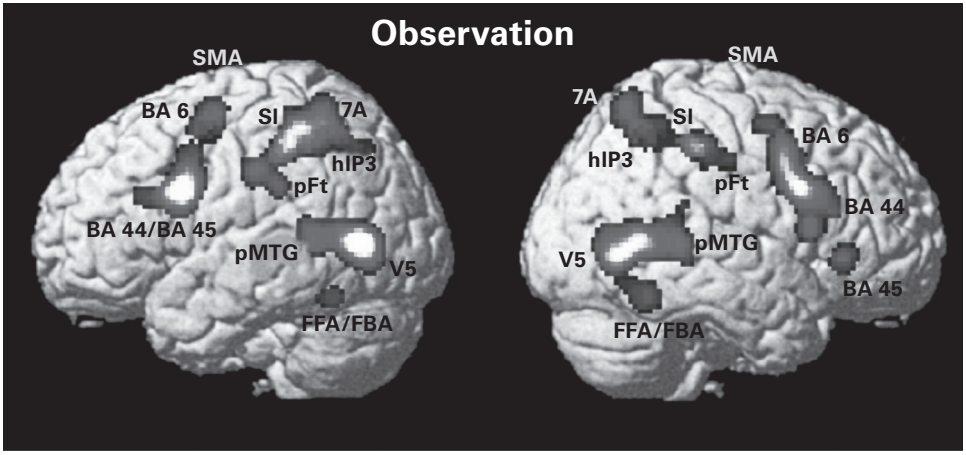

Figure 8.2
Cortical areas active during action observation in humans. Lateral view of the two hemispheres of a human brain showing the areas activated in neuroimaging studies during action observation. Data from a meta-analysis made on 87 studies. The three main nodes of the action observation circuit are the posterior part of the superior temporal sulcus; the inferior parietal lobule, including the intraparietal sulcus, plus the adjacent part of superior parietal lobule; the premotor cortex, mainly its ventral part, plus the posterior part of the inferior frontal gyrus. (Modified from Caspers, S., Zilles, K., Laird, A. R., Eickhoff, S. B. [2010]. ALE meta-analysis of action observation and imitation in the human brain. *NeuroImage*. 50, 148–167. © Elsevier 2009, with permission from Elsevier.) (See plate 2.)

observation of grasping actions regardless of whether they are performed by a human hand, a robot hand, or even a tool (Peeters et al., 2009; see also Gazzola, Rizzolatti, Wicker & Keysers, 2007). Second, listening to action-related sounds activates the same areas (Lewis et al., 2005; Gazzola, Aziz-Zadeh & Keysers, 2006; see also Lewis et al., 2011).

It is worth noting here that a clear link exists between the capability to produce specific actions and that of recognizing sounds related to them. Patients with limb and buccofacial apraxia were asked to match sounds evoking human-related actions with specific visual pictures. A double dissociation was found. Hand-action-related sound recognition was specifically impaired in limb apraxia, while mouth-action-related sounds were impaired in buccofacial apraxia (Pazzaglia, Pizzamiglio, Pes & Aglioti, 2008).

What Are Mirror Neurons For?

The question quite obviously arises as to why the motor system should be endowed with a mechanism encoding the goal of actions performed by others. The original interpretation was that the mirror encoding allows the observers to understand the actions of others *directly* (di Pellegrino et al., 1992; Rizzolatti, Fadiga, Gallese & Fogassi, 1996; Gallese et al., 1996). Observing other people performing a given motor act elicits a motor activation in the observers' brain similar to that occurring when observers themselves plan and execute that action. The similarity between these two motor activations concerns the goal of the observed and planned action. Because of this similarity, observers are able to understand others' actions without the need for any inferential processing (Rizzolatti et al., 2001; Rizzolatti & Sinigaglia, 2008).

Two studies in which the goal-relatedness of the observed movements could be understood in the absence of visual information provided clear support for this interpretation. The first study presented two conditions: in one, the monkey saw the experimenter's hand moving toward an object to grasp it; in the second, the same reach-to-grasp motor act was performed by the experimenter, but the monkey was prevented from seeing the final hand-object interaction because the latter was hidden by a screen (Umiltà et al., 2001). In the second study, monkeys listened to the sounds of a motor act (such as ripping a piece of paper) without seeing it (Kohler et al., 2002). The results showed that in both experiments, F5 mirror neurons fired in the absence of proper visual information. The neuron activation therefore reflected the comprehension of the goal of another's motor act, regardless of the sensory information describing it.

Alternative Views on the Mirror Neuron Function

In spite of these findings, some researchers have argued that mirror neuron activation does not subserve others' action understanding; rather, it provides, at most, a motor emulation based on a goal representation present outside the motor areas endowed with the mirror mechanism (Csibra, 2007; Jacob, 2008, 2009). In this regard, it is worth noting that the authors who play down the importance of the mirror neurons for action understanding usually suggest that goal encoding is *primarily* due to the higher-order visual areas such as those located in STS, a region known to be involved in the visual analysis of others' actions in both monkeys and humans (Perrett et al., 1989; Allison, Puce & McCarthy, 2000; Puce & Perrett, 2003; Jellema & Perrett, 2005).

There is no doubt that STS neurons play a fundamental role in encoding others' motor acts. It is, however, highly unlikely that they might subserve action understanding by themselves, with the parieto-frontal mirror network playing only an ancillary role in this function. The reasons are the following.

First, a cortical region responsible for action understanding should be characterized by the capability to encode the goal-relatedness of others' motor behavior with the highest degree of generality. This capability characterizes the parieto-frontal mirror neurons, but not the neurons of STS. Parieto-frontal mirror neurons encode the goal of the observed motor acts regardless of whether they are performed with the mouth, hand, or even tools. This does not occur in STS.

Second, theoretical reasons indicate that STS neurons cannot, by their nature, generalize the goal of an observed action. In fact, because they are STS visual neurons, it is hard to understand how they could encode the visual features of a hand performing a motor act *and* those of a mouth performing the same motor act. Postulating an association process similar to that described for the temporal lobe is not helpful because goal generalization is *not* based on the spatiotemporally adjacent visual representations necessary to achieve a visual association as that described in the inferior temporal lobe (Miyhashita, 1988; Sakay & Miyhashita, 1991). Conversely, mirror neurons, by virtue of their motor goal encoding, can be activated by different visual stimuli (e.g., hand and mouth actions) provided that they share a common goal (e.g., grasping). The presence of a motor scaffold is a necessary condition for action generalization that goes beyond what is achievable by mere visual association.

A recent study provides empirical evidence in favor of this point (Cattaneo, Sandrini & Schwarzbach, 2010). The study was based on a TMS

adaptation paradigm (Silvanto, Muggleton & Walsh, 2008). Its rationale was that transcranial magnetic stimulation of a given area "dishabituates" the features encoded by the neural population of that area, which were previously "adapted" by repetitive stimulus presentation. In the study by Cattaneo et al., participants were presented with "adapting" movies of a hand or foot acting on different objects and asked to compare as quickly as possible a motor act shown in a test picture to the adapting movies. TMS pulses were delivered over the ventral premotor cortex bilaterally, the left IPL and the left STS. The results showed that the delivery of TMS over both premotor and IPL cortices shortened the reaction times to adapted stimuli, regardless of the effector performing the observed motor act; in contrast, TMS stimulation of STS induced shortening of reaction times for adapted motor acts, but only when the effector was the same.

Mirroring and Understanding Action

Granted that mirror neurons are critically involved in encoding the goal of others' actions, some questions still remain to be answered. What type of action understanding do mirror neurons really subserve? How does the mirror-based action understanding differ from other action understanding types?

Understanding Actions without Using the Mirror Mechanism

It goes without saying that the claim that the mirror mechanism plays a crucial role in understanding the behavior of others does not imply that no other mechanisms are involved in this function. Some of them may rely on the association between a given stimulus and its effect. For example, one can understand a gesture conveying a threat without necessarily transforming it into a motor format. A monkey is scared when it sees the experimenter throwing a stone at it, even if the way in which the stone is thrown does not correspond to the way in which the monkey would throw it (Wood, Glynn, Phillips & Hauser, 2007; Wood & Hauser, 2008). This is not surprising because what counts here is the painful effect of being hit by the stone rather than the precise gesture mirroring.

On the other hand, a long tradition accounts for action understanding by referring to the capability of individuals to "read" the minds of others, that is, to attribute a causal role to their mental states (such as beliefs and desires) in representing and executing actions. The nature and the format of this "mind reading" are still a matter of controversy (Carruthers &

Smith, 1996; Malle et al., 2001; Goldman, 2006; Hutto & Ratcliffe, 2007). There is, however, no doubt that human beings have this capability.

Understanding from the Inside

A fundamental difference distinguishes the mirror-based action understanding and the understanding of others' behavior relying either on a lower-order associative mechanism or on a higher-order meta-representational capability. An example could be helpful in this regard. Imagine that a skiing instructor is demonstrating how to turn left or right. The instructor is a playful individual. Thus he likes, from time to time, to deceive his students by performing bodily movements that, although compatible with the demonstrated action, are not the most appropriate ones. You are an absolute beginner, while your friend Peter is a good skier. That the instructor is doing something strange will immediately be understood by Peter, who will ask the instructor what this bizarre movement is for, while you will be unable to recognize whether the observed movement is appropriate or not.

It is skiing knowledge that allows Peter to understand the instructor's behavior. Such an understanding, however, is not grounded in a mere associative mechanism, nor does it imply any explicit mentalizing. There is no reason to assume that you are less able than your friend to read the mind of the instructor by meta-representing him as having certain propositional attitudes to account for the fact that you cannot actually understand *what* the instructor is doing. What counts here is the capability to understand the goal-relatedness of the observed movements on the basis of one's own motor repertoire. We have called this kind of understanding "understanding *from the inside*" (Rizzolatti & Sinigaglia, 2010).

This simple example tells us that the richer our motor repertoire is, the greater is our sensitivity to others' actions. This theoretical conclusion is supported by a large number of fMRI studies (Buccino et al., 2004; Calvo-Merino et al., 2005, 2006; Cross, Hamilton & Grafton, 2006; Haslinger et al., 2006; Aglioti, Cesari, Romani & Urgesi, 2008). Research has shown, for example, that viewing videos of classical ballet or of capoeira activates differently the brain areas endowed with the mirror mechanism of participants, depending on whether they were experts in one or the other type of dancing (Calvo-Merino et al., 2005, 2006; see also Cross et al., 2006). Similar results have also been obtained in a series of experiments on other types of skilled actions such as playing the piano (Haslinger et al., 2006) or basketball (Aglioti et al., 2008), thus demonstrating that the activation of the brain areas endowed with the mirror mechanism during action observation depends on the observer's motor expertise.

From Goal to Intention Understanding

The mirror mechanism plays an important role in understanding not only others' motor acts but also the motor intentions behind those acts. In fact, compelling evidence suggests that parietal and frontal mirror neurons are involved in encoding not only *what* others are doing (i.e., the goal of the observed motor acts) but also *why* others are doing what they are doing (i.e., the intention behind it).

Single-cell recordings from IPL (mostly area PFG) and from the ventral premotor cortex (area F5) of the monkey showed the existence of a specific set of neurons that discharge in association with specific motor acts but are activated maximally when the encoded motor act is part of a specific action ("action-constrained" neurons; Fogassi et al., 2005; Bonini et al., 2010). For example, an action-constrained neuron might strongly discharge when the monkey is grasping a piece of food for bringing it to the mouth, but not when the monkey is grasping a piece of food for placing it in a container (fig. 8.3; see plate 3).

Many action-constrained neurons are endowed with the mirror mechanism (Fogassi et al., 2005; Bonini et al., 2010). These neurons selectively discharge both when the monkey interacts with an object within the frame of a specific action and when it observes a motor act as part of the same specific action (e.g., grasping-for-eating but not grasping-for-placing). Their activation therefore provides information not only on what an individual is doing (e.g., grasping) but also, and most importantly, on why the individual is likely to do it (for eating or for placing). By virtue of this mechanism, the observer, besides understanding the observed motor act, is also able to anticipate what the motor intention underlying the whole action is. In other words, the observer is able to understand the motor intention with which the agent is doing what he is doing.

Evidence also indicates that the mirror mechanism plays a crucial role in intention understanding in humans. Brain-imaging studies showed that recognizing the motor intention behind a given motor act activates the right frontal and parietal nodes of the mirror network (Iacoboni et al., 2005; Hamilton & Grafton, 2008). More recently, the temporal dynamics of brain activations were investigated in individuals observing hand motor acts (i.e., grasping a mug) by using high-density electrical neuroimaging. The acts were presented within or without a context. The instruction was to understand the motor intention with which the presented acts were performed (e.g., grasping for drinking or for moving away) (Ortigue, Sinigaglia, Rizzolatti & Grafton, 2010). The results showed a pattern of brain activation characterized by an initial recruitment of the left posterior

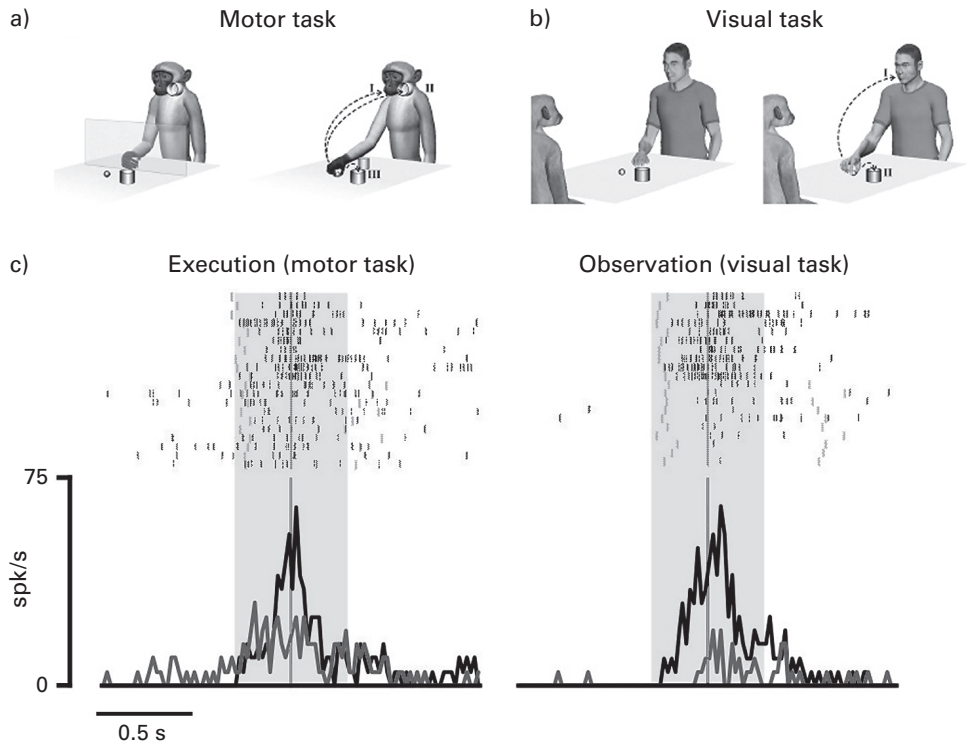

Figure 8.3

Example of an F5 mirror neuron modulated by action intention. (a) Paradigm used for the motor task. The monkey, starting from a fixed position, reaches and grasps a piece of food, then brings it to the mouth (I, grasp-to-eat), or places it into one of the two containers (II/III, grasp-to-place). (b) Paradigm used for the visual task. The experimenter, starting from a fixed position, reaches and grasps a piece of food, then brings it the mouth (I, grasp-to-eat) or places it into a container (II, grasp-to-place). (c) Discharge of the neuron during execution (left) and observation (right) of the two actions. Rasters and histograms are aligned (green vertical lines) on the contact between the monkey's or experimenter's hand with the object. Red: neuron discharge during grasp-to-eat condition; gray: neuron discharge during grasp-to-place condition. Blue bars indicate the onset of the hand movement; yellow bars indicate the contact between the hand and the container in the grasp-to-place condition. (Modified from Bonini, L., Rozzi, S., Serventi, F. U., Simone, L., Ferrari, P. F. & Fogassi L. [2010]. Ventral premotor and inferior parietal cortices make distinct contribution to action organization and intention understanding. *Cerebral Cortex*, 20, 1372–1385, by permission of Oxford University Press.) (See plate 3.)

temporal and inferior parietal cortices followed by activations of the right temporo-parietal region. The authors suggested that the early left hemisphere activation was due to the recruitment of a lateralized mirror network mediating the understanding of the goal of object-directed motor acts. The later right hemisphere activation would indicate the involvement of this hemisphere in understanding the intention of others.

Most interestingly, an EMG study (Cattaneo et al., 2007) demonstrated, although indirectly, that motor intention encoding in humans is based on an organization similar to that found in monkeys. In one condition, children were instructed either to grasp a piece of food so as to eat it, or to place it into a container; in another condition, they had to observe an experimenter performing the same actions. The activity of the mouth-opening mylohyoideus (MH) muscle was recorded. The results showed that in the grasping-for-eating condition, both the execution and the observation of eating actions produced a marked increase of MH muscle activity as early as during the reaching phase. In contrast, no MH activity was found in the execution and observation of placing actions (fig. 8.4).

As for action understanding, claiming that the mirror mechanism plays an important role in processing others' intentions is not tantamount to stating that mirror-based intention understanding covers all varieties of understanding others' intentions. Nor does it involve the assumption that every kind of intention understanding depends on (or is related to) the activation of the mirror mechanism. What the mirror mechanism tells us is that the mirror-based intention understanding is based on the same organization of motor representations that enable one to perform a given motor act (e.g., grasping) with a given intention (grasping *for* bringing to the mouth or *for* moving away) (Rizzolatti & Sinigaglia, 2007; Gallese, 2007; Sinigaglia, 2009).

Mirroring Action and Space

Spatial Modulation of Mirror Neuron Responses

The studies of the mirror mechanism we have discussed until now were focused on how this mechanism contributes to the understanding of the actions performed by others. Are there other action features that mirror neurons encode?

A single-neuron study recently addressed this issue by investigating whether the spatial relations between agent and observer might influence the mirror neuron activity. Mirror neurons were recorded from area F5 and

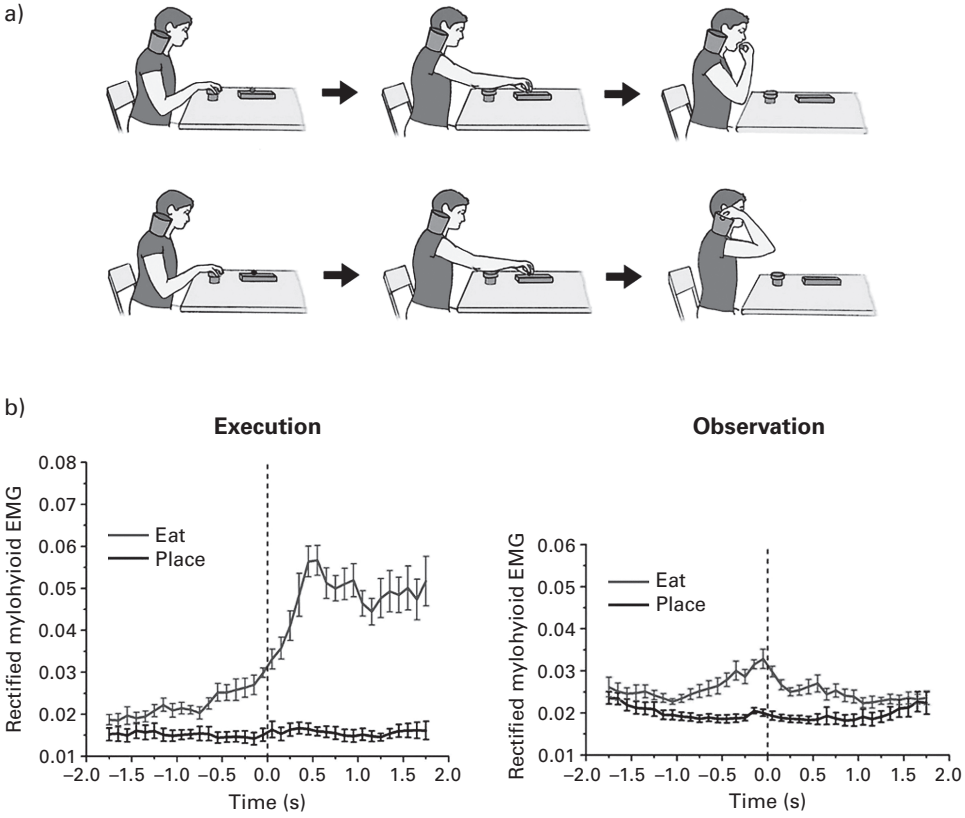

Figure 8.4

Activity of the mylohyoid muscle during execution and observation of two actions in children. (a) Representation of the two actions. *Upper part*: The child reaches for and grasps a piece of food, brings it to the mouth, and eats it. *Lower part*: The child reaches for and grasps a piece of paper and puts it into a container placed on his shoulder. (b) *Left*: Time course of the EMG activity of the mylohyoid muscle during execution of grasping for eating (pale gray) and grasping for placing (dark gray). *Right*: Time course of the EMG activity of the mylohyoid muscle during observation of grasping for eating (pale gray) and grasping for placing (dark gray). Vertical bars indicate the standard error. The curves are aligned (dashed vertical line) with the moment in which the object is lifted. (Modified from Cattaneo, L., Fabbi-Destro, M., Boria, S., Pieraccini, C., Monti, A., Cossu, G., & Rizzolatti, G. [2007]. Impairment of actions chains in autism and its possible role in intention understanding. *Proceedings of the National Academy of Sciences*, 104, 17825–17830. © The National Academy of Sciences of the USA.)

tested while the monkey observed the experimenter grasping objects within the monkey's reaching distance (peripersonal space) or outside its reach (extrapersonal space) (Caggiano et al., 2009). The results showed that about half of the recorded neurons were differentially modulated by the spatial location of the observed motor act. Some neurons preferred actions executed in the monkey's peripersonal space, while others discharged strongly for extrapersonal space stimuli.

Most interestingly, space selectivity did not always reflect the physical distance between the observer and the agent. A consistent percentage of recorded F5 mirror neurons changed their space selectivity when a transparent barrier was interposed between the observing monkey and the object target of the action. Thus some neurons, which did not respond to the grasping actions carried out near to the monkey but responded to grasping performed in the extrapersonal space, fired to near stimuli after the introduction of the transparent barrier. In contrast, other F5 mirror neurons responding to grasping actions carried out near to the monkey ceased to fire when the transparent barrier was introduced. These findings indicate that the spatial selectivity of some F5 mirror neurons could not construed in terms of physical nearness and farness but depended on the possibility for the monkey to reach for, and to act on, the object that was a target for others' actions.

What might be the purpose of this mechanism? Spatial selectivity does not appear to play a critical role in action understanding, so why should goal encoding be modulated by the observer's action space and action possibility?

The Peripersonal Space as an Action-Related Space

To answer this question, it may be useful to examine the functional properties of neurons encoding peripersonal space. Peripersonal space is defined as the space within the agent's reach (Rizzolatti, Matelli & Pavesi, 1983). A large amount of evidence suggests that such a space is represented in a parieto-frontal network whose main nodes are found in area VIP inside the intraparietal sulcus and area F4 in the ventral premotor cortex. Neurons encoding peripersonal space were also found in areas PF and PFG (Rozzi et al., 2008).

Area VIP contains two main classes of neurons responding to sensory stimuli: purely visual neurons and bimodal (visual and tactile) neurons (Colby, Duhamel & Goldberg, 1993; Duhamel, Colby & Goldberg, 1998). The tactile receptive fields of VIP bimodal neurons are located predominantly on the face (Colby et al., 1993; Duhamel et al., 1998). The visual receptive fields are typically in spatial register with the tactile ones.

Neurons of area F4 are motor neurons discharging in association with monkeys' movements such as arm reaching or head orientation toward or away from the stimuli (Gentilucci et al., 1988). Many neurons of area F4 also respond to sensory stimuli. They might be unimodal (purely somatosensory neurons), bimodal (somatosensory and visual) (Gentilucci et al., 1988; Fogassi et al., 1992, 1996a, 1996b; Graziano, Yap & Gross, 1994), or more rarely trimodal neurons (i.e., neurons responsive in addition to auditory stimuli) (Graziano, Hu & Gross, 1997).

The visual receptive fields of most F4 neurons do not change position with respect to the observer's body when the eyes move (Gentilucci et al., 1983; Fogassi et al., 1992, 1996a, 1996b; Graziano et al., 1994). Thus the visual responses of these neurons encode visual stimuli not in retinal but in bodily coordinates (Gentilucci et al., 1988), mapping them in frames of reference that are anchored to different body parts (Fogassi et al., 1996a, 1996b). They move when the corresponding body part moves (Graziano et al., 1997).

Peripersonal space, however, cannot be explained just in terms of mere cross-modal integration. The peripersonal space is dynamic in nature and intrinsically action related (Rizzolatti, Fogassi & Gallese, 1997). Studies have shown that the extension of the visual receptive fields of F4 neurons increases in depth when the speed of an approaching stimulus also increases (Fogassi et al., 1996a). The advantage of this dynamic mapping of space is evident: the earlier the neuron discharges, the earlier the motor act encoded by it is evoked. This enables an efficient mapping of what is really near, allowing one to take advantage of a positive opportunity or to avoid a threat.

Further evidence in favor of the organization of the peripersonal space in terms of goal-directed actions comes from studies on peripersonal receptive fields during tool use. In a seminal paper, Iriki, Tanaka, and Iwamura (1996) showed that the extent of the visual receptive fields of monkeys' parietal neurons changes during actions involving tool use. They trained monkeys to retrieve pieces of food using a rake. They found that when the rake was used repeatedly, the visual receptive fields anchored to the hand expanded to encompass the space around the rake. If the animal stopped using the rake but continued to hold it, vRFs shrank back to their normal extension. Similar results have been obtained by Ishibashi, Hihara, and Iriki (2000).

Taken together, these data indicate that peripersonal space is body centered and motor in nature, and above all, its multimodal integration and body-centeredness can be fully understood only in relation to the possibility to act. It is such a relation to action that allows one to understand the

dynamic nature of the peripersonal space as a space primarily involved in subserving bodily interactions with the surrounding objects. This relation to action may also help in explaining why the mirror mechanism could be differentially activated according to whether the target of another's action falls within or outside the observer's reaching space.

Because of its intrinsic action-relatedness, the peripersonal space embodies the varying range of our motor potentialities, encompassing all of what is literally ready to our hands. Thus the finding that the visual responses of a subpopulation of mirror neurons exhibit a spatial selectivity that cannot be understood in terms of physical distance suggests that mirror goal encoding of others' actions might provide observers with critical information for organizing and coordinating their future behavior with respect to what other people are doing. In other words, by mapping the observed actions onto the reachable or the out-of-reach space, the mirror mechanism might contribute not only to understanding the behavior of others but also to enabling one to respond appropriately to an upcoming threat or to an approaching offer for cooperation.

Mirroring the Peripersonal Space of Others

It has recently been demonstrated that the mirror mechanism might reflect the peripersonal space of another individual. Single neurons were recorded from monkey VIP. The studied neurons exhibited tactile receptive fields and visual receptive fields in spatial register with the tactile ones. The extent of the peripersonal receptive field of each neuron was delimited. Then the stimulus was presented outside of it, at a distance of 120 cm. No visual response could be elicited at this distance. However, if an experimenter, standing in front of the monkey at this distance from it, waved his hand close to his own body part that corresponded to the one where the monkey tactile receptive field was, the response appeared. The responses disappeared if the experimenter moved away (Ishida et al., 2010).

This study is of great interest because it shows that the mirror mechanism in the area VIP codes body-directed rather than object-directed motor acts as in the PFG/AIP-F5 circuit, thus suggesting a fascinating explanation of how individuals encode the body of others. Note that although Ishida and colleagues have not studied the motor responses of the recorded neurons, the area VIP is strictly connected with the area F4, where peripersonal space is encoded in terms of movements. It is therefore plausible that the responses that appear to be visual actually represent potential motor acts directed toward specific bodily parts (Gentilucci et al., 1983; Fogassi et al., 1996a).

Is the Mirror Mechanism Dependent on the Observer's Point of View?

Finally, an intriguing single-neuron study (Caggiano et al., 2011) recently showed that the relationship between the mirror mechanism and space is even more complicated than previously thought. The visual responses of F5 mirror neurons were recorded while the monkey was watching movies showing object grasping from three different visual perspectives: the monkey's point of view (0°), a lateral view (90°), and a frontal view (180°). The results showed that most of the tested mirror neurons (74 percent) exhibited a view-dependent activity with responses tuned to specific points of view. The remaining neurons (26 percent) exhibited view-independent responses.

This result has interesting implications for highlighting the role of mirror neurons in action understanding. As discussed earlier, we have convincing evidence in favor of a hierarchy of action-processing steps with STS involved in elaborating the visual details of the observed actions, and the areas containing the mirror mechanism (PFG/AIP and area F5) transforming this visual information into a motor format. This format is instrumental for understanding action goals.

The presence of view-invariant mirror neurons in the area F5 is consistent with this account. It is plausible that they implement the top level of a hierarchy that encodes observed actions in terms of their motor goal independently of action-specific visual characteristics.

Somewhat more difficult is the interpretation of the responses of the view-dependent mirror neurons. A possibility is that view variance is not resolved at lower levels, as is STS, but also requires the view-dependent mirror neurons in area F5 in the formation of view-invariant representations within area F5. The generation of view invariance by pooling the responses of view-dependent neurons is a well-established mechanism in object recognition in the ventral pathway (Logothetis & Sheinberg, 1996; Tanaka, 1996) and in several computational models (Poggio & Edelman, 1990; Oram, Perrett & Hietanen, 1993; Tarr & Bulthoff, 1998).

This interpretation, however, presents some difficulties. Mirror neurons are motor neurons, and what is recorded is their output, that is, a motor signal. This signal remains the same regardless of how a neuron is triggered. Imagine that a grasping mirror neuron in F5 sends an output to two F1 (M1) neurons, one controlling the flexion of the thumb, the other the flexion of the index finger. During voluntary movements, these two neurons will be activated anytime the neuron in F5 fires. When the same F5 mirror neuron is triggered by a visual stimulus (the vision of grasping), those two F1 neurons will again be activated. It is irrelevant whether the

firing of the F5 mirror neuron is due to the "will" of the agent, to the vision of a grasping hand seen from a given perspective, or even to the sound of an action. The result is identical: an activation of the F5 neuron and a subsequent activation of the neurons located in the primary motor cortex. In other words, visual information *triggers* mirror neurons, but the specific sensory information conveyed by this triggering input is lost once the postsynaptic potentials are transformed into action potentials. Thus a simple "visual" explanation of these findings does not appear to be likely.

An alternative interpretation is that view-dependent mirror neurons, in spite of their motor nature, play a role in encoding the visual perspective of the observed actions. The circuit in which the area F5 is embedded includes, in addition to outputs toward motor centers, connections to the inferior parietal lobule, which further projects to the superior temporal sulcus (STS). These connections could be instrumental to the integration of visual information encoded in STS with motor knowledge represented in the premotor cortex. Consistent with this hypothesis are some behavioral data demonstrating modulations of the visual perception of action by concurrent or preceding motor behavior (Craighero, Fadiga, Rizzolatti & Umiltà, 1999; Blakemore & Frith, 2005; Wilson & Knoblich, 2005; Casile & Giese, 2006; Schütz-Bosbach & Prinz, 2007). Simultaneous recordings from premotor and higher-order visual areas are obviously required to prove this hypothesis. Yet this hypothesis is extremely attractive, and its testing could clarify the role of feedback connections in the mirror circuits.

Conclusion

It has long been traditional to consider the motor system as a system devoid of any cognitive function. The data reviewed in this chapter indicate that this view is untenable. They show that a series of cognitive functions such as space and action recognition not only require the activity of motor areas but are deeply embedded in motor organization. In particular, action understanding relies on the recruitment of motor resources that originally evolved for motor behavior and subsequently became the substrate for understanding others from the inside.

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9 Beyond Serial Stages for Attentional Selection: The Critical Role of Action

Glyn W. Humphreys

Introduction

The cognitive revolution in experimental psychology emerged in the 1950s. One critical topic for cognitive theories was the role of central limitations on information processing, even when peripheral limitations in perceiving the stimulus and in making the required response were not present. A classic example of this is dichotic listening, where two messages are played simultaneously, one to each ear (Broadbent, 1958). If participants are instructed to attend and respond to one ear, performance at repeating the attended message can be good; on the other hand, participants may be quite unable to report the unattended message. Changing the instruction to attend to the other ear, however, allows that message to be reported, but this occurs at the cost of reporting the message on the other ear. This example illustrates that each message is perceptible, and each can be responded to—so the limits in performance are not due to stimulus degradation or an inability to respond; rather, there is a central problem when both messages have to be processed simultaneously and made available for response. One account of this central limitation is that information processing depends on a limited set of resources, which are insufficient for processing and responding to multiple stimuli at any one time. Owing to this limitation, participants must select one message and ignore the other, to enable at least one stimulus to be responded to appropriately. The study of selective attention is concerned with the processes involved in selecting and responding to one among the multiple stimuli.

Much of the initial work on selective attention was concerned with determining the processing stage at which selection occurred. Early selection theories proposed that, to prevent an overload of processing resources, irrelevant stimuli had to be filtered out at an early stage—before the irrelevant stimuli made contact with stored knowledge (e.g., Broadbent, 1958).

In contrast, late-selection theorists (Deutsch & Deutsch, 1963) argued that all stimuli (whether attended or not) received high-level processing (e.g., making contact with stored knowledge), but irrelevant stimuli were filtered out at a stage of response selection. Between these two extremes, other authors (e.g., Treisman, 1960) took a more flexible approach, suggesting that there was degraded processing of unattended stimuli, so that they were less likely than attended stimuli to access stored knowledge. However, under appropriate conditions (e.g., if the preceding context primed the representations for the stimuli or if the stimuli had a low threshold for accessing stored knowledge, as might be the case for your own name; Moray, 1959), then unattended stimuli might still access stored knowledge. However, the basic question of why processing should be limited, given the huge processing capacity available at a neural level, did not receive much consideration.

In work proceeding from a ZiF research group at Bielefeld University in 1984–85, researchers began to raise the question as to why information processing should be so constrained (e.g., see Allport, 1987; Neumann, 1987). One proposal suggested that processing is constrained because humans are limited in the number of actions that can be performed at one time. Given the limited number of effectors we possess and the requirement of having effectors work together, some constraints on information processing are necessary so that (at least under most circumstances) only the behaviorally relevant stimuli are available to control action. We have only two hands, two legs, one head—and coherent action would not emerge in an organism unless there was control over which stimuli gained access to the limited effector systems. In addition, it was argued that at least two forms of selection may be distinguished: the selection of which object to act on at any one time, and the selection of which action to assign temporary priority when a response is made to the selected object (Allport, 1987; Neumann, 1987). This distinction, between object and action selection, has been mirrored by neurophysiological arguments about the distinction between posterior and anterior attentional systems in the brain (Posner & Petersen, 1990). How object and action selection might interrelate, however, was less clearly set out. Do these different forms of selection operate serially in time, with, for example, object selection preceding action selection? Or might the processes involved in object and action selection interact, so that the processes involved in action selection modulate object selection? Does preparing a particular action (priming which action is selected) affect which object is selected when multiple objects are present?

In this chapter, I consider work that has emerged since the argument of "attention for action" was made. I suggest that the main tenet of the argument arising from the ZiF research group remains correct: attention does (at least in part) reflect the need to perform coherent actions, and this involves both selecting the appropriate object to act on and the appropriate action. In addition to this, however, I propose a dynamic view of selection in which the processes of object and action selection interact, rather than operating at discrete stages when we act on the world. This dynamic view of selection adds extra detail to the argument from the original ZiF group by showing not only that selection is *for* action but also that constraints from action permeate even early stages of object selection. I present evidence for this argument in three sections. First, I discuss results showing that preparation to act influences selection at a perceptual stage of processing. This can be thought of as a form of feedforward processing, from action preparation, to constrain perceptual coding. Second, I present evidence that our perceptual systems are sensitive to action-related properties of objects, even in the absence of any explicit preparation for action. My suggestion here is that, due to learning of statistical regularities in the environment related to action, object selection is inherently action related. That is, the object selection system is "tuned" to respond to action-related cues. Third, I review data indicating that any effects of tuning the object selection system to action properties of the world are themselves enhanced by motor preparation. Action is inherent to the way that selective attention operates. At the close of the chapter, I sketch an account of why it may be useful for selection to be modulated by action couched in terms of predictive coding.

1 Feedforward Effects of Action Preparation

Several lines of evidence suggest that the preparation to make a motor action to one location in space modulates the selection of stimuli at that location. Some of the most elegant work on this idea has been reported by Deubel, Schneider, and colleagues (e.g., Deubel & Schneider, 1996; Deubel, Schneider & Paprotta, 1998; see Schneider & Deubel, 2002, for a review). In their original procedure, participants were required to program an eye or a hand movement to one location following an initial cue. As the action was being prepared, but before it was carried out, a visual target was briefly presented. Deubel, Schneider, and colleagues reported that participants made better identifications of the visual target if it fell at the same location as where the action was programmed to end, relative to when it fell at a

different (nonmatching) location. This result occurred even when the visual target always fell at a set location, which should have allowed participants to decouple their attention to the target from the action—for example, holding attention at the location where the target was expected while programming the movement to another location. The results demonstrate that this decoupling was not achieved, since programming the action still affected target discrimination. From this it can be argued that an obligatory coupling exists between programming an action and object selection: programming an action to one location directs attention there even if the task is to select an object at a different location. Since these original demonstrations, this group (e.g., Baldauf & Deubel, 2010) has gone on to show that the coupling of attention to programmed action is not tied to single actions: if multiple consecutive actions are planned, there can be enhanced report of targets at each end location of the different actions. The effects are not confined to immediate action; rather, the planning of a number of actions can prime selection of objects at several locations for at least some time after the actions are programmed. The planned actions seem to feed forward to modulate the landscape of locations where object selection subsequently takes place. The effects have also been shown to generalize across modalities. For example, having participants program a saccade to a location on an arm facilitates detection of a tactile stimulus presented there (Juravle & Deubel, 2009). Apparently planning an action to a location enhances the selection of coincident objects, irrespective of the modality through which the objects are presented.

Other work shows that the effects of action programming on attention are not limited to the spatial location(s) where the action(s) should end. Linnell et al. (2005), for example, had participants prepare to point to one among a number of circles, and neighboring circles might or might not be connected together. As reported by Deubel, Schneider, and colleagues, discrimination was enhanced when targets fell at the end location of the programmed action. In addition, Linnell et al. found that there was enhanced discrimination of targets that fell in an uncued circle, provided it connected to a circle to which the action was programmed; no such enhancement occurred when the target appeared in another uncued but unconnected neighboring circle. In this case, the effects of action on attention were mediated by grouping the visual elements into a single perceptual object (when the circles connected relative to when they were separate). Action enhanced selection of the whole object (the grouped circles), even if the action was programmed only to a part of the object (one of the two grouped circles).

The work of Deubel, Schneider, and colleagues with normal participants has also been shown to modulate the performance of patients with brain lesions, where particularly striking effects have been reported. Kitadono and Humphreys (2007), for example, assessed the effects of planning a pointing action on the report of visual targets by two patients with damage to posterior parietal cortex (PPC) who suffered visual extinction. Patients with extinction are able to detect single stimuli presented in either visual field but fail to detect contralesional stimuli (falling on the side opposite their lesion) when ipsilesional items are presented simultaneously to compete for attention (Karnath, 1988). The extinction effect can be attributed to the lesion biasing the processing of the ipsi- and contralesional stimuli. While a weakened contralesional stimulus can be detected when presented alone, it will lose out in any competition to be selected when presented simultaneously with a stronger ipsilesional stimulus (Duncan, Humphreys & Ward, 1997). Kitadono and Humphreys reported that when patients showing extinction programmed a pointing response to the contralesional side, the report of targets there improved by as much as 80 percent under extinction conditions (when another item was presented on the ipsilesional side). These data suggest that motor preparation by the patients fed forward to enhance object selection on the affected (contralesional) side, and this helped the patients overcome the lesion-induced bias to the ipsilesional side. Subsequently Kitadono and Humphreys (2009, 2011) showed that the beneficial effects of having the patients prepare to act could be sustained over multiple pointing responses (similar to the findings of Baldauf & Deubel, 2010, with normal participants). In addition, performance was examined when the patient had to make a pointing response to one location (e.g., to the ipsilesional side) while the target *always* appeared on the opposite side (e.g., at a contralesional location). As with normal participants (Deubel et al., 1998), report of the visual targets was affected by preparation of an action to a mismatching location (e.g., report of a contralesional target dropped when an ipsilesional pointing action was prepared, relative to when no action was prepared). If the patients could ignore the prepared action, their performance should be equated across conditions when there was no action and when there was an action programmed to the opposite side. That the prepared action affected object report indicates that the action could not be ignored, and it automatically affected object selection.

These effects of action preparation on attention can be accommodated by the premotor theory of attention, which proposes that all forms of attentional selection reflect the feedforward of neural activation from brain

regions involved in motor planning to those mediating sensory processing (Rizzolatti, Riggio, Dascola & Umiltà, 1987). However, other neuropsychological data indicate that this may not be the full story. Khan et al. (2009), for example, reported the case of another patient with PPC damage who could program eye movements accurately into his contralesional visual field but showed no evidence of enhanced discrimination of a target at the end location of the eye movement (see also Blangero et al., 2010). Here programming of the eye movement was spared, but attentional biases linked to the action were impaired. The opposite pattern was reported by Kitadono and Humphreys (2007) with one of their patients (patient MH). MH had the disorder of optic ataxia, where there is inaccurate pointing to visual targets. Despite actual pointing being inaccurate, MH showed facilitated report of targets appearing at the intended end location of the action (and the facilitation decreased when the target appeared at another location). In this case, generation and control of the action were damaged, but attention was still shifted to the location where the action should have occurred. These data suggest that attention-related effects are coupled to action programming but are distinct from the action itself. These neuropsychological data refine the work on action programming and attention in normal participants, indicating that there is a distinction between effects of attention stemming from the generation of an actual motor action and from the internal programming of action. There can be appropriate motor action without effects of internal programming on attention (Khan et al., 2009), and there can be appropriate effects of internal programming of action even when the motor action itself is impaired (Kitadono & Humphreys, 2007).

As well as modulating attention to space, action programming has also been shown to "tune" perceptual processing to particular stimulus features. This was first demonstrated in a neuropsychological context. Humphreys and Riddoch (2001) reported a patient with unilateral visual neglect who was extremely impaired at detecting named targets if they fell on his contralesional side. However, detection of the same items was much improved if the patient was cued to search based on an action description ("find an object to drink from" rather than "find the cup"). This benefit for searching by action arose only when the objects were oriented appropriately for action (e.g., when the handle of the cup was oriented to the patient), suggesting that detection depended on the presence of action-related properties of objects meshing with the expectation for action. Duncan and Humphreys (1989) suggested that visual search involves matching incoming stimulus information against a template of the expected target. From

the results of Humphreys and Riddoch (2001), one can suggest that an action template, perhaps based on action prepared by the patient, is distinct from templates that may be derived from an object's name (e.g., specifying the semantic properties of an object).

This result has been elaborated by Bekkering and Neggers (2002). These investigators had normal participants carry out visual search tasks and make either a grasping or a pointing response to a target defined by a conjunction of color and orientation (e.g., a red vertical rod among green vertical and red horizontal rods). When the task was pointing, the first saccade made by participants tended to go to a distractor carrying the color of the target (e.g., a red horizontal distractor). In contrast, when the task was grasping, the first saccades went more frequently to distractors that had the same orientation as the target (e.g., green vertical distractors). Bekkering and Neggers proposed that preparation for a particular action biases attention toward stimulus attributes that are compatible with that action (grasping biasing attention to orientation rather than color).

Effects on the processing not only of stimulus orientation but also of size have been reported by Symes, Tucker, Ellis, Vainio, and Ottoboni (2008). They had participants prepare to make either a power or a precision grip response on detection of a change to a set of objects varying in size. The changes were difficult to detect, as they were masked by flashing all the display on and off when the change occurred (Simons, 2000). When a power grip was prepared, a change to a large object was far easier to detect than a change to a small object. In contrast, when a precision grip was prepared, a change to a small object was detected more easily than a change to a large object. The data again indicate that attention is sensitive to the action that is prepared; there is enhanced attention to objects whose properties are congruent with the prepared response. Other work further indicates that action preparation may differentially weight a whole perceptual dimension, perhaps alongside any weighting of specific features within the dimension (as in Bekkering & Neggers, 2002; Symes et al., 2008). Wykowska, Schubö, and Hommel (2009) (see also Fagioli, Ferlazzo & Hommel, 2007), for instance, suggest that having to make a grasp response facilitates search for size-defined targets, while having to make a point response facilitates search to luminance-defined targets.

In all the foregoing examples, the preparation for action appeared to benefit performance—for example, facilitating the detection of stimuli that match an action template and otherwise might go undetected (e.g., Humphreys & Riddoch, 2001). In other cases, though, action preparation can disrupt target detection. Müsseler and colleagues (e.g., Müsseler & Hommel,

1997a, 1997b; Müsseler, Wühr & Prinz, 2000) had participants detect a briefly presented right- or left-oriented arrow after having prepared a left- or right-hand response. In this case, detection was worse for the compatible visual stimulus matching the motor response, relative to when the stimulus did not match it. This blindness to a response-compatible stimulus was interpreted in relation to the common-coding theory of Prinz (1992, 1997). This theory proposes that both perceptual stimuli and planned actions use the same (common) internal codes, and generation of one code by an action may impair the concurrent generation of the same code from perceptual input. The net result is that attention to (and perception of) the compatible visual stimulus is disrupted. To some degree, we might suppose that common coding is a prerequisite of any theory that supposes that perceptual coding can be modulated by action preparation. Whether performance is facilitated or disrupted by generation of this common code may depend on the timing of motor preparation and stimulus coding. With preactivation of a motor response, the data indicate that coding of compatible stimuli is facilitated. Performance may be disrupted, however, if the codes are derived concurrently (Müsseler & Hommel, 1997a, 1997b; Müsseler et al., 2000).

2 Attention to Action Properties of Stimuli

As well as attention being affected by action preparation, evidence is also mounting for attention being modulated by what we might term "action properties" in images: visual properties of objects that are strongly associated with object use or with interactions between one object and other objects when they are being used together. These effects can occur when participants do not explicitly prepare a motor response. I begin with a neuropsychological example. Di Pellegrino, Rafal, and Tipper (2005) tested patients with left-side extinction. They presented pictures of cups whose handles were turned to the right or left. When the cup in the left field had its handle on the left, extinction was reduced. Di Pellegrino et al. suggested that the presence of the handle on the left of the left-side cup evoked a motor response to the stimulus, which helped the patients direct attention to that side, reducing extinction (cf. Kitadono & Humphreys, 2007). The effect did not appear to be due to the handle making the left-side cup visually salient. In a control study, Di Pellegrino and colleagues replaced the handle with another salient visual cue (a patch equated for position, size, and luminance to the handle) and failed to find any recovery from extinction. The data suggest that attention in the patients could be drawn to the action-related property of the cup (its handle). J. J. Gibson (1979)

coined the term "affordance" to refer to our perceptual response to action-related properties of objects in the environment. Here the data suggest that when the left cup was oriented with its handle on that side, attention was drawn to the affordance of the cup for action.

These effects are not confined to affordances from single objects. Riddoch et al. (2003) tested patients showing visual extinction with pairs of objects that were either oriented together as they would be when being used (the action-related condition) or positioned such that they could not easily be used together (the action-unrelated condition; see fig. 9.1[a] vs.

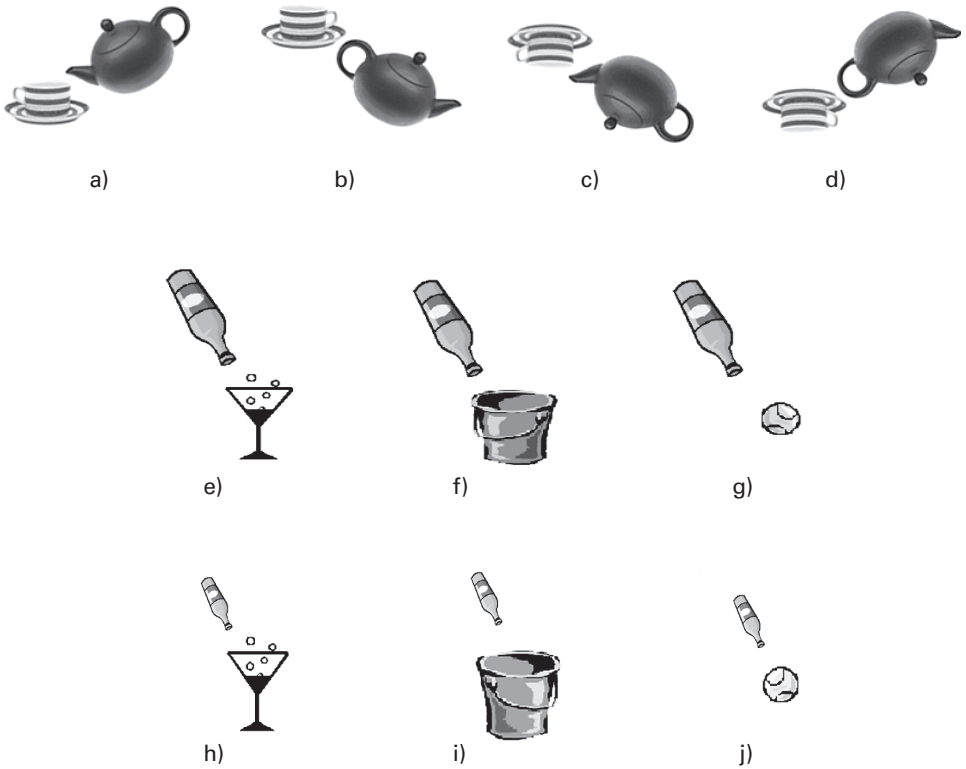

Figure 9.1
Example stimuli used in studies of extinction based on action relations between stimuli: (*a*) an upright action-related pair; (*b*) an upright action-unrelated pair; (*c*) an inverted action-related pair; (*d*) an inverted action-unrelated pair; (*e*) stimuli that are action related and familiar as a pair; (*f*) stimuli that are action related and unfamiliar as a pair; (*g*) stimuli that are not strongly interacting and are unfamiliar as a pair; (*h*)–(*j*) stimuli from the same conditions as (*e*)–(*g*) except that the relative size of one object is altered in relation to the other.

[b]). One object appeared in the left field, and the other in the right. The patients showed less extinction when the objects were positioned to interact with each other (fig. 9.1[a]) relative to when they were positioned not to interact (fig. 9.1[b]). The patients in Riddoch et al. made few errors on single-item trials, suggesting that the effects of action relations were not due to guessing based on the item in their ipsilesional field (seeing a teapot pouring and guessing that there must also be a cup; this guessing strategy would generate errors on trials when a single ipsilesional stimulus was present). Minimal effects on extinction occurred when the objects were associatively related but would not be used together. Riddoch et al. proposed that interacting (action-related) objects grouped together, reducing the effects of any attentional bias to select the ipsilesional item. That is, the presence of action relations between the stimuli caused the stimuli to be coded as a perceptual unit and selected together.

In the original study of Riddoch et al. (2003), the action-related objects were also visually familiar as a pair. Were the effects driven by the action relations between the stimuli or by the visual familiarity of the upright pairs? Riddoch et al. (2006) assessed this question by comparing extinction with action-related objects that were familiar or unfamiliar as pairs (fig. 9.1[e] and [f] respectively), relative to a baseline where the objects were neither strongly action related nor familiar as a pair (fig. 9.1[g]). Extinction was reduced most strongly when the objects were both familiar together and action related, but it was still reliably reduced (compared with the action-unrelated and unfamiliar baseline) for action-related but unfamiliar pairs. These data indicate that positioning objects to interact together can be sufficient to reduce extinction. Indeed, the mere familiarity of object pairs is not sufficient. Humphreys, Riddoch, and Fortt (2006) found that placing two objects in familiar locations with respect to each other (a sun above a palm tree) produced no benefit compared with when the same objects were placed in unfamiliar locations in relation to each other (sun below the palm tree).

In a further extension of this work, Riddoch et al. (2011) assessed whether the perceptual unit formed by interacting objects was coded configurally—in the sense that the elements had to appear in their familiar overall orientation and had to have the appropriate relative sizes to interact together. In studies of face processing, configural information (reflecting the relations between individual features) is extracted most readily when the stimuli are upright, and this coding is sensitive to the relative sizes of the features (Biederman & Kalocsai, 1997). Riddoch et al. demonstrated that the reduced extinction effect, shown when patients reported two

action-related stimuli, was found when the stimuli were upright, but not when the same items were inverted (fig. 9.1[a] and [b] vs. [c] and [d]). Similarly reduced extinction was reported only when the objects were the same relative sizes (good report for fig. 9.1[e] and [f], but not for [h]–[j]). These data suggest that action-related objects have to be coded together as a single configuration for extinction to reduce.

How might this sensitivity to action relations come about? One proposal is that the sensitivity reflects statistical learning of the events taking place in the world (Humphreys & Riddoch, 2007). Actions determine events, and different events are distinguished on the basis of an action that changes one situation into another. Statistical learning may be sensitive to the cues that distinguish one event from the next. Since actions between two objects will convey more statistical information to distinguish events than the mere presence of noninteracting objects in the environment, then the interactions between objects may come to be learned as perceptual units. Activation of the same perceptual unit by two interacting objects will enable the objects to be selected as a single perceptual unit rather than as two competing objects, and hence the effects of spatial bias on extinction reduce.

Roberts and Humphreys (2010a) examined the neural basis of the effects of action relations in an fMRI study. They used a 2 x 2 x 2 design applied to stimuli containing two objects and two scenes (fig. 9.2). Participants were asked to attend to, and make decisions about, the objects (are these objects related?) or the scenes (both city, both country, or city and county?). The objects were familiar as a pair or not, and they were positioned for action or not.

Roberts and Humphreys found that both the left lateral occipital complex (LOC), an area associated with responses to high-level properties of object shape (Kourtzi & Kanwisher, 2001), and the left fusiform gyrus showed greater activation to objects positioned for action than to objects not positioned for action (fig. 9.3). In the LOC, the greater activity for action-related stimuli was not affected by the familiarity of the pairs, whereas it was found only for familiar pairs in the left fusiform region. Both regions showed greater activation for action-related pairs when the objects were attended, but the increased activity for action-related pairs remained even when the objects were unattended (albeit only for familiar pairs, in the fusiform gyrus). These results are interesting in several ways. First, they demonstrate that activation differences for action-related over unrelated pairs are found in ventral cortical regions associated with object recognition, rather than in the more dorsal occipito-parietal regions associated with action (cf. Goodale & Milner, 2004). Apparently sensitivity to

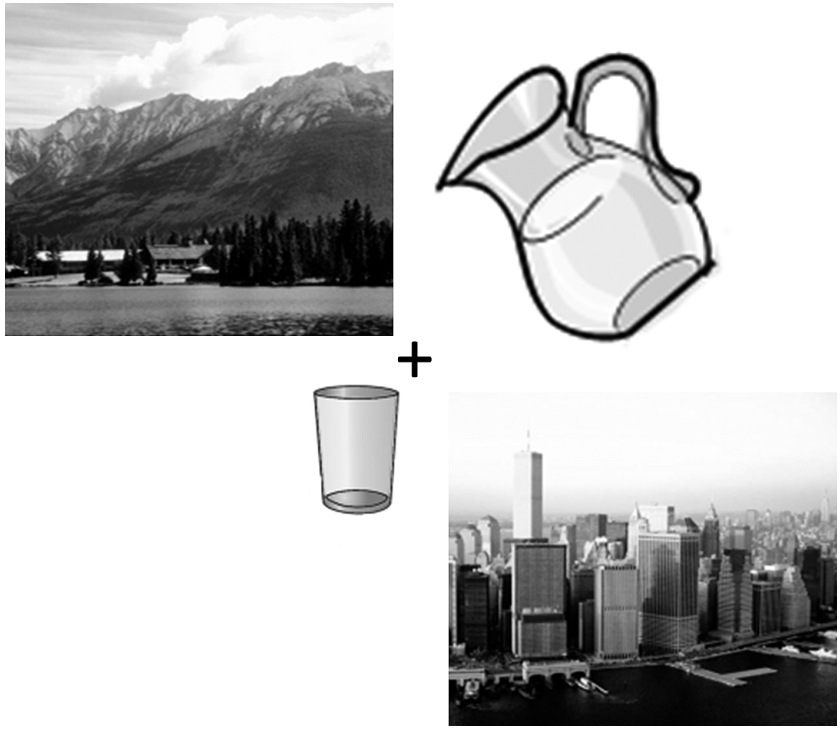

Figure 9.2
Displays used by Roberts and Humphreys (2010a). Participants made decisions about whether the objects were related (attend condition) or the scenes were both city or country landscapes (unattended condition for the objects). The objects could be familiar as a pair or not, and they could be positioned for action or not. Here a familiar pair is shown positioned for action.

the positioning of objects for action is something the object recognition system is tuned to. This would fit with the argument that sensitivity to action relations is acquired through statistical learning. Second, the data show that some brain regions are relatively immune to the familiarity of the objects as a pair, registering more whether the pair is positioned for action (the LOC); in contrast, other brain regions are tuned only to familiar pairs positioned for action (left fusiform gyrus). There are effects both of action relations and of the familiarity of the objects as a pair. Third, the neural response to action-related objects occurs even when the objects are not fully attended (e.g., when participants are asked to attend to the scenes rather than the objects). These last results fit with the neuropsychological

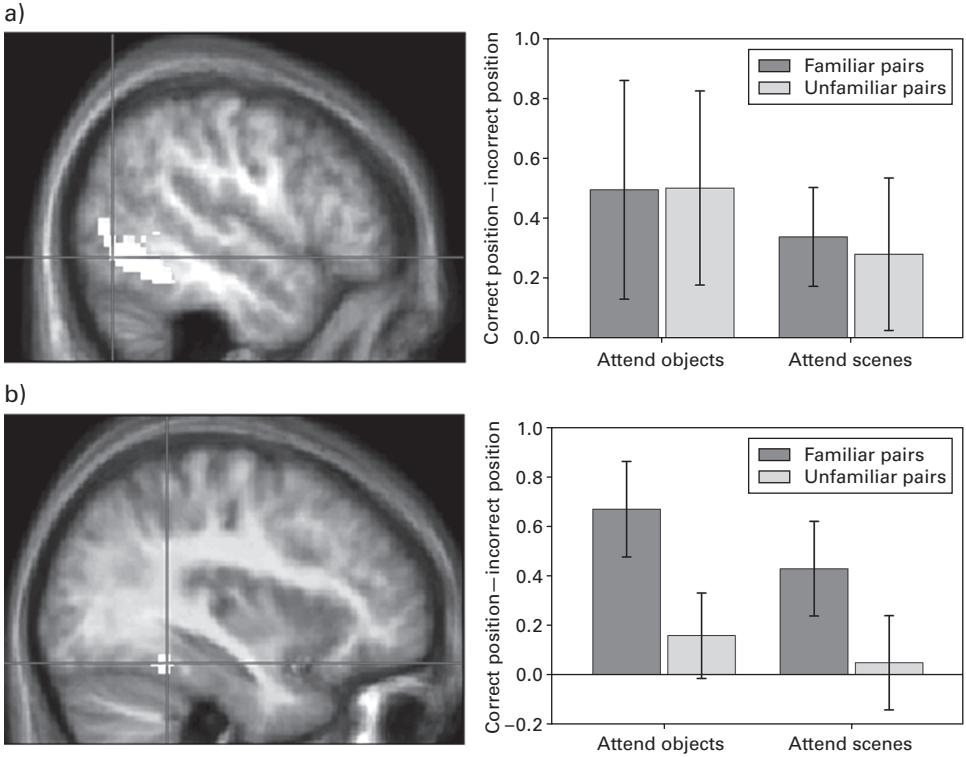

Figure 9.3
The results from Roberts and Humphreys (2010a) showing greater brain activity for action-related over action-unrelated pairs of objects. (*a*) Activation in the lateral occipital complex (LOC), which is affected by action positioning and attention, but not the familiarity of the object pairs. (*b*) Activation in the left fusiform gyrus, which is affected by action positioning and attention, but only with familiar object pairs.

data where (i) extinction patients who do not attend fully to contralesional stimuli are still affected by action relations between stimuli in the ipsi- and contralesional fields, and (ii) there are effects both of positioning objects for action and the familiarity of the pairs (Riddoch et al., 2006). It is also interesting that the extinction patients reported by Riddoch et al. (2003, 2006, 2011) had parietal lesions that did not compromise the ventral visual areas activated by action relations in Roberts and Humphreys (2010a). This fits with the idea that the effects of action relations may reflect activation within the ventral stream, which in turn helps the patients select both objects for perceptual report.

Although I have emphasized the data from patients showing extinction here, it is important to note that the effects of action relations between objects are not confined to neuropsychological patients. Green and Hummel (2006), for example, had normal participants verify whether the second of two object images matched a name given at the start of each trial. They found that verification was more accurate when the first image was another object that was typically used with, and shown in interaction with, the second object. This effect of positioning the objects for action occurred only when a short interval elapsed between the stimuli, under which circumstance perceptual integration between the objects was maximized. These data suggest that verification of the target was enhanced when the objects formed an integrated unit in interaction with each other.

Effects of interactions between separate objects have also been shown to generalize to include interactions between body parts and objects, indicating sensitivity (for example) to whether an object is gripped correctly for action. Yoon and Humphreys (2005) had participants make object decision responses (is this a real object or not?) to stimuli that were shown along with a hand, which gripped the stimuli either correctly or incorrectly for action. Although the hand grip was irrelevant to the task, participants were affected by grip congruence; for instance, reaction times to objects were faster when the grip was congruent for the action that would normally be performed on the object (a power grip to the handle of a hammer) relative to when the grip was incongruent (a pinch grip to the handle of the hammer).

Other evidence for enhanced attention to the action-related properties of interacting objects comes from studies of temporal-order judgments (TOJs) in normal participants. Participants' ability to judge the temporal order in which objects are presented is affected by attention; objects that are attended tend to be judged as appearing earlier relative to objects that are not attended (Shore, Spence & Klein, 2001). In neuropsychological patients, lesions can bias processing on one side of space. When patients with a spatial bias in attention have to make TOJs, they tend to judge that items on their ipsilesional side appear before items on the contralesional side (Rorden, Mattingley, Karnath & Driver, 1997). In addition, TOJs are sensitive to grouping. When two objects group, TOJs become more difficult, leading to a flattening of the function for discriminating which object came first and which second (essentially, if two objects appear as a single unit, then we need longer interstimulus intervals before we can judge which came first, so the slope of the discrimination function becomes less steep; Nicol & Shore, 2007). Roberts and Humphreys (2010b) had normal

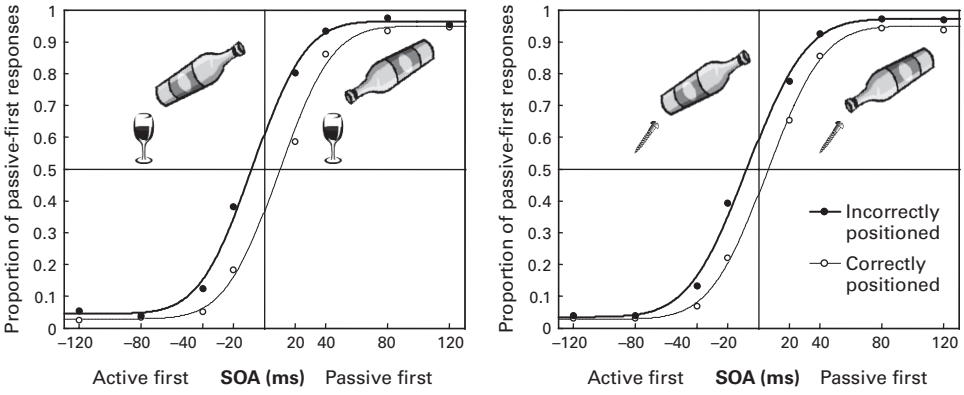

Figure 9.4
Stimuli and results from Roberts and Humphreys (2010b). The data show the proportion of trials on which the passive object was reported first. For both familiar object pairs (*a*) and unfamiliar pairs (*b*), correctly positioning the objects for action led to more trials where the active object was reported as appearing first (curve shifted to the right).

participants make TOJs for pairs of objects that were either correctly or incorrectly positioned for action (fig. 9.4). They found that correctly positioning objects for action did not flatten the discrimination function (as would be expected if grouping between action-related objects influenced the TOJs), but it did lead to a constant shift in which the "active" object tended to be judged as appearing first—the active object being the stimulus that would be manipulated when an action took place (see Riddoch et al., 2003). This result held with both familiar and unfamiliar object pairs. The lack of a grouping effect here may be due to the TOJ task emphasizing attention to individual objects (as it requires participants to decide which object comes first). Irrespective of this, the shift to judge that active items appear first, when the objects are positioned for action, indicates that attentional priority is given to these objects when an action relation is detected. Here positioning of the active object for action enhanced processing even when the active object did not group with its partner. This last finding can also be related back to the neuropsychological data. Riddoch et al. (2003) noted one interesting result in their extinction study, which arose on the error trials when participants only reported one of the two objects present. With objects not positioned for action, the patients consistently reported the objects on their ipsilesional side when extinction took place (consistent with their spatial bias in attention). However, when

the objects were positioned for action, a different result occurred. In this case, patients tended to report the active object in the pair irrespective of its location; this means that the patients sometimes reported the active object from their contralesional field, and there was then extinction of the object falling in the ipsilesional field. This bias to reporting the active object irrespective of the field of presentation is consistent with an attentional bias to this item when an action relation is computed, as it occurred only when an action relationship was present. Note also that the data suggest that the action relationship was computed implicitly; the report errors occurred when the patients were unaware of one of the objects, and which object they were unaware of was determined by an action relationship that they could not report.

Taken together, these data indicate that attentional selection is sensitive to the action relations between stimuli. Two objects positioned to interact together, or objects depicted with a congruent or incongruent grasp for action, tend to be selected as a single perceptual unit—a process that is sensitive to the objects appearing in their normal orientation and having appropriate relative sizes. This effect occurs with objects that are unfamiliar as a pair, but is stronger with familiar object pairs. The effect survives effects of PPC lesions that generate spatial biases in visual selection, and it is mediated by activation within the ventral visual stream, consistent with visual statistical learning of action relations. I suggest that action-related cues in the visual environment enhance object selection even when an explicit action is not prepared by participants.

3 Action Preparation and Action Relations between Objects

I have argued that visual attention responds to action properties of single and multiple interacting objects even when an explicit action is not generated. However, this does not mean that the response to action-related properties in an image cannot be modulated by activation fed forward from the action system. I now evaluate whether evidence shows that feedforward effects from action preparation interact with any visual effects of action relatedness. Humphreys et al. (2010) reported preliminary evidence for this in a study of the effects of seeing a grasp action depicted on an object. As already noted, Yoon and Humphreys (2005) established that the congruence of a grasp action affected reaction times to an object. Humphreys et al. (2010) measured EEG responses when participants carried out object decisions to the stimuli used by Yoon and Humphreys (2005). EEG signals carry certain signatures of the stages of processing at which an effect

is occurring. One such signature is termed "desynchronization of the mu rhythm." EEG activity in the mu frequency range (8–13 Hz) becomes desynchronized (so that different electrodes show different firing patterns) when people prepare a motor action (Pfurtscheller & Aranibar, 1979), and this desynchronization of the mu rhythm provides a signature of preparation to act. Humphreys et al. (2010) reported that desynchronized mu activity increased over regions of motor cortex in the left hemisphere when participants made object decisions to congruent relative to incongruently gripped objects. This result is consistent with congruently gripped objects evoking preparation of a motor action. It is striking that the maximum desynchronization was observed very rapidly after the onset of the stimulus (between 100 and 200 ms after the onset of the display). This result suggests that, in addition to any visual response to the action-related stimulus (the type of response measured in Roberts & Humphreys's 2010a fMRI study), there may also be a rapid motor response to action-related properties of an image.

This evidence from EEG is supported by fMRI data using the same stimuli. Along with their EEG study, Humphreys et al. (2010) also reported data from fMRI when object decisions were made to congruently and incongruently gripped objects. Both visual and motor regions of the brain showed a differential response to objects depicted with congruent relative to incongruent grips. Notably there was differential activity both in the LOC (see also Roberts & Humphreys, 2010a) and in dorsal premotor cortex—a brain area linked to preparation for action. The results suggest that there can be enhancement of the response to action information in an image based on the internal activation of an observer's motor system, particularly brain areas mediating preparation to action. Whether the motor and visual components of the effects emerge independently or whether they interact (e.g., with the visual component being enhanced by feedback from an activated motor response) is an important issue that has yet to be fully addressed. Nevertheless the data indicate that any enhanced visual response to action relations between objects can be accompanied by an enhanced response within the motor system.

Conclusion

The results I have reported present consistent evidence for the close coupling of action and attention. In the first section, I reported evidence that the preparation to act enhances visual processing for objects falling at the end location of the action. A prepared action also "tunes" selection to favor

stimulus attributes consistent with the response. This typically enhances the perception of stimuli that are congruent with the prepared action, but it can disrupt perception if the stimulus and response codes are generated concurrently. The processes that link attention to action appear to reflect an attentional response to planned action, but not necessarily the action itself (against a strict premotor account of the data). In the second section, I showed that even without preparation of an explicit action, attention is sensitive to action-related properties of images. For example, interacting pairs of objects appear to be selected together, as do objects and appropriately interacting body parts (a hand grasp). At a neural level, these effects are associated with activity in visually responsive areas of ventral cortex (e.g., the LOC). In the third section, I presented evidence that the effects of having action-related information in an image can themselves be linked to the activation of the motor system in the brain; most notably, activation of dorsal premotor regions in the left hemisphere occurs when images contain action information that is congruent rather than incongruent with an object. These dorsal premotor regions are linked to preparation to make a motor response.

Theoretical Implications: Action as Predictive Coding

The results presented here highlight not only that selective attention serves the constraints of action but also that the mechanisms of selection themselves are strongly determined by action-related properties of the world and by the actions we plan to effect. The picture that emerges runs counter to the idea that selection operates at one of a serial set of processing stages, for example, when there is perceptual encoding of objects or selection of the response to make to an object. Rather than thinking, then, that there are functionally distinct stages of object and action selection (Posner & Petersen, 1990), we must instead conceive of these processes as being highly interactive. For instance, activation of a given response to an object may feed forward to bias perceptual processing in favor of matching features. Selection then emerges as a dynamic process, constrained by properties of objects, the actions we are able to perform, and the state of activity within the object and response selection systems.

One point to note is that the discussion I have presented has focused exclusively on the interaction between manual action and attentional selection, and the important topic of how other forms of action—including spoken language—may also affect how attention operates. It is interesting to note here that emerging evidence suggests that what we attend to can be determined as strongly by a verbal description as by a visual representation of a

target, even when the verbal description is irrelevant for the task (e.g., Soto & Humphreys, 2007). This suggests that language too can prime the perceptual system to respond to matching features. Whether this happens through automatic translation of words into their associated semantic concepts, or through a more active process of imagery, is a question for future research.

What might be the advantages for having visual selection modulated by action? One reason for attention and action being closely coupled is that action may provide an important form of "predictive coding" that facilitates the rapid processing of our highly complex environment. Friston, Mattout, and Kilner (2011), for example, suggest that the internalization of information about actions being performed in the world, and the mapping out of our own future action trajectories, provide ways of predicting environmental change; in this way, action coding can help formulate attentional selection as a process of active inference. For example, preparing to make a particular action to an object will predictively prime the perceptual system to selectively extract features related to the action, which, if confirmed, can directly be mapped into a response, speeding behavior. Similarly, statistical visual learning of action-related features and of action-related associations between objects can reduce the demands of independent processing of objects, in turn enabling the interacting objects to be selected together or action programming to be sensitive to both objects (e.g., when a bimanual action is made to correctly positioned knives and forks). Evidence suggests that visual grouping of objects facilitates bimanual action (e.g., Edwards & Humphreys, 2002), and action-based grouping (Humphreys & Riddoch, 2007) may be particularly useful for generating coordinated responses to pairs of objects. My suggestion, then, is that action preparation forms a particular form of predictive coding that is highly useful because it initiates the links between a stimulus and a response, making stimulus-driven behavior more efficient.

Acknowledgments

The work reported in this chapter was supported by the BBSRC and ESRC (UK).

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IV Development

10 Action in Infancy: A Foundation for Cognitive Development

Claes von Hofsten

Introduction

How does our ability to think and reflect on the world emerge? I like to argue that action is the foundation for this process. It is essential for all aspects of cognition including social understanding. It reflects the motives of the child, the problems to be solved, the goals to be attained, and the constraints and possibilities of the child's body and sensory-motor system.

Actions are defined by goals and not the specific procedures by which they are implemented. They are initiated from within by motives and not from the outside as reactions. Most important, they anticipate what is going to happen next and prepare the organism for the upcoming events.

The movements of even the simplest animals, like the earthworm, are organized as actions (Darwin, 1881). Darwin showed that earthworms covered their burrows very tightly with pieces of leaves and other artifacts when the weather was dry but provided only sloppy coverings when the weather was damp and rainy. Thus this behavior, although primitive, has a goal (to adjust the covering) and a motive (to accomplish optimal moisture). It is initiated from within the organism and not just elicited like reflexes are. The same is valid for the behavior of newborn infants. Their movements are founded on perception and knowledge of upcoming events. If mastery of actions relies on acquiring such information, then the development of actions has to do with acquiring systems for handling such information (von Hofsten, 1993, 2003, 2004, 2007). It has to do with anticipating one's own posture and movements, as well as perceiving objects and events in the world and understanding other people's actions.

Perception is needed both for planning actions and for guiding them toward their goals. Therefore actions are not possible before there are perceptual systems that provide the necessary information for controlling

them. Converging evidence indicates that all sensory systems are available from birth and can be used to guide basic forms of actions. The sensory system that has been least exercised is the visual system, because the light that reaches the eyes is only minimally structured in the womb. However, although visual acuity at birth is only 3 to 5 percent of the adult capacity, it provides sufficient resolution for perceiving the gross features of other people's faces and controlling manual actions.

However, action not only relies on perception but also is a necessary part of the perceptual process. For instance, active touch is required to haptically perceive the form of an object. The hand must move over the object and feel its form, its bumps, and its indentations (Gibson, 1966). The clearest example of the necessity of action for functional perception is vision itself. Our visual field consists of a very small fovea surrounded by a large peripheral visual field over which acuity rapidly deteriorates with increasing angular eccentricity. In spite of this, we have an illusion of seeing equally clearly over our whole visual field because the eyes and head are always prepared to turn to where attention is directed.

Although perception and action are mutually dependent, there is an asymmetry between them. Action is a necessary part of perceiving, but only in a general sense. It provides opportunities for perceiving and guides the perceptual system to where the information is. However, it does not tell the perceptual system what to perceive. This has clear consequences for development. The ability to extract the necessary information must be there before actions can be organized. Only then can infants learn to control the dynamics of their motor system and gear it to the appropriate information. Take, for instance, the speech system, where infants' ability to perceive the phonemic and prosodic structure of speech develops much ahead of their ability to produce those sound qualities (Menn, 1983).

In this chapter, I argue that all actions are predictively controlled; that is, they are founded on knowledge of what is going to happen next. This is possible because events in the world are governed by rules and regularities. Perception and cognition have to do with knowing the rules of prediction and using them to regulate actions. At least three kinds of prediction rules must be taken into account: those related to the physical world, those related to one's own actions, and those related to other people's and animals' actions. They all rely on perceiving motion and change and on timing actions to these external events. The child is endowed with motives and learning principles that are specifically geared to explore the rules of prediction. As children learn how to control their own actions, they also

begin to be able to take other people's actions into account by perceiving their goals and motives.

The Necessity of Predictive Control

Behavior geared to the outside world has to deal with the fact that events precede the feedback signals about them. In biological systems, the delays in the control pathways may be substantial. The total delays for visuomotor control, for instance, are at least 200 ms in adults and substantially longer for infants (Gredebäck, Örnkloo & von Hofsten, 2006). Relying on feedback is therefore nonadaptive. The only way to control actions successfully is to predict what is going to happen next and use that information to control one's movements.

Furthermore, most events in the world require us to move to specific places at specific times while being prepared to do specific things. This requires us to foresee the ongoing stream of events in the world, as well as how our own actions unfold. Time is irreversible, and what has been accomplished is only of interest for the ability to control the next part of an action. The development of action is therefore both a question of building procedures for structuring movements ahead in time and procedures for extracting the right kind of predictive information for the detailed monitoring of actions (Johnson, 2000).

Predictive control is possible because events in the world are governed by rules and regularities. The essence of perception and cognition has to do with knowing those rules and using them to regulate actions. There are at least three types of rules.

1. Rules that regulate the events in the physical world. The most general rules are laws of nature like inertia and gravity. They always apply. Other important physical rules are those that apply to spatial relationships and numbers. To successfully interact with the physical world, subjects must take these rules into account.
2. Rules that regulate one's own body movements. Many muscles interact in complex ways in the execution of every movement. Taking those relationships into account is absolutely necessary for being in control of the body. The rules that regulate body movements presuppose knowledge of the rules that regulate the physical world.
3. Rules that regulate the interactions among individuals. These rules are about interpreting the social signals that inform us about other people's emotions and intentions. The social rules and regularities are the most

complicated to understand and master. They presuppose knowledge of the rules that regulate movements and physical events.

Predispositions for Predictive Control

Infants have knowledge of the rules that regulate physical phenomena, their body movements, and social interactions from an early age and use them to guide their actions. These rules are part of what Spelke (2000) has called *core knowledge*, which provides the bootstrapping for perceptual, cognitive, and action development.

The function of these predispositions, in addition to enabling the newborn child to act, I suggest, is to provide activity-dependent input to the sensory-motor and cognitive systems. This makes it possible for newborn infants to begin exploring the relationship between commands and movements, between vision and proprioception, and to discover the possibilities and constraints of their actions.

Core Principles of Perceiving the External World

Knowledge of the world is ultimately based on perception of the rules that regulate the physical world (see rule 1). All the various modes of perception function at birth in more or less sophisticated ways. The olfactory sense is, for instance, surprisingly good. When newborn infants were exposed to their mother, who had one breast thoroughly washed and one that was not, significantly more infants spontaneously selected the unwashed breast rather than the washed alternative (Varendi, Porter & Winberg, 1994). In the auditory domain, studies show that newborn infants turn the head toward a sound source (Muir & Field, 1979), indicating the ability to externalize sounds. They also prefer their mother's voice (deCasper & Fifer, 1980). Newborn infants' visual perception is remarkably good considering that little stimulation has been provided in the womb. The resolution suffices for perceiving the major features of faces and objects. A crucial question is whether newborn infants are able to perceive objects, because objects are of crucial importance for adjusting to the visual world. To be able to visually perceive objects, the optical flow around us must be divided into units with inner unity and outer borders that exist over time, extend behind other objects, and move on continuous trajectories (see, e.g., Spelke, 1998). Successful interaction with the physical world is founded on such knowledge. Some of it is present in the newborn child.

Core Movement Principles

Movements of neonates have traditionally been discussed in terms of reflexes rather than actions. According to Sherrington (1906), a reflex is a hardwired sensory-motor loop organized at a spinal or para-spinal level. Although reflexes serve important functions, they are stereotyped and elicited and, once launched, run their predetermined course. In other words, they cannot be considered goal directed, and they do not adjust to future states in a predictive way. This means, for instance, that reflexes are not subject to learning. Neither are they adjusted to meet other goals or attain other advantages than those for which they were originally adapted.

Like adults, neonates have reflexes. For instance, a slight hit below the kneecap elicits a stretch reflex. However, most of the so-called neonatal reflexes are not characterized by the properties just described. On the contrary, neonatal movements are functional, goal directed, and flexible in the sense that they can be altered to gain advantage. The newborn child is clearly prepared to interact with the external world and adapt to it. Rooting, for instance, is traditionally described as a typical neonatal reflex. It refers to the infant's search for the nipple of the breast. Mechanical stimulation in the area around the mouth makes the infant move his or her mouth toward the point of stimulation (Prechtl, 1958). However, rooting is more than a simple reflex. Rooting is not elicited when the infant touches itself (Rochat & Hespos, 1997), but only when an external object is the source of stimulation. Furthermore, a newly fed infant is less likely to perform these movements. These facts speak in favor of a more sophisticated organization of this behavior than suggested by the reflex notion.

Newborn infants anticipate the sensory consequences of their actions and move in smooth and continuous ways. This is both a spatial and a temporal task, and we can therefore conclude that the brain has already worked out many of the basic principles for movement production at that age. To be in control, however, movements are simplified. For instance, muscles are controlled not individually but as synergies involving a number of muscles. An example of this is the extension-flexion synergy of the arm and hand of newborn infants; that is, muscles in the limb extend and flex together.

Sucking is probably the most precocious behavior of the newborn. It may be the only one for which the newborn is more skilled than the adult. Skilled sucking relies on a complex interaction of muscle contractions that are predictive in nature. Within a day or so after birth, the sucking system functions with amazing accuracy (Craig & Lee, 1999). Such smooth functioning relies on adjusting the change in sucking pressure to the flow of milk that is different from suck to suck. In other words, the newborn infant

has to sense the coming flow of milk and to adjust the sucking pressure to it ahead of time.

Apart from using sucking to acquire food, neonates are also able to use sucking to gain other advantages, for instance, as a means to get access to the mother's voice (deCasper & Fifer, 1980) or to regulate a visual event (Kalnins & Bruner, 1973). DeCasper and Fifer found that, within a day from birth, neonates would alter their sucking rate to access to their mother's voice. This shows that newborn infants can use behaviors as means rather than ends and can flexibly apply them to a variety of problems.

Newborn infants also control the movements of their arms. Von Hofsten (1982, 1984) showed that neonates extend their arms toward an attractive object in front of them. When the infants fixated the object, they moved their arms closer to it than otherwise. They also tended to open up their hands as they extended the arms. This is not a preparation for grasping the object but rather a part of a more general extension synergy that optimizes the possibility of encountering the object with the hands (fig. 10.1). In other words, objects attract the attention of neonates, who expect them to have sensory consequences for the hands.

Van der Meer (1997) provided another important demonstration that neonates control their arm movements. She positioned a narrow beam of light that passed in front of an infant in a situation where the surroundings were otherwise dark. She measured spontaneous arm-waving movements while the infant lay supine. When the neonates happened to put their hands into the light beam, the light was reflected on their hands.

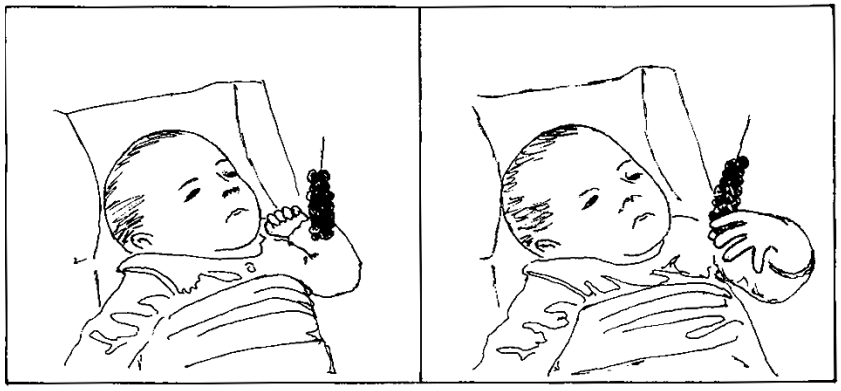

Figure 10.1
A week-old infant looking at and reaching for an object in front of him. He did not grasp the object but opened the hand during the extension of the arm.

The infants would then maintain the hand longer in the light than was expected by chance. When the position of the beam was altered, the neonates moved the hand to the new position of the beam. This implies that the neonates were able to visually control the movements of that hand in a crude way. This is remarkable, considering that vision has not been available in the womb, except maybe when the fetus moves the hand or arm in front of the eyes. Then a shadow is formed, and the movement of that shadow across the visual field might be associated with the action of the arm.

Evidence also indicates that the goal-directed arm and hand movements in neonates are predictive. When neonates put a thumb into their mouth, they open the mouth in anticipation of the thumb's arrival (Lew & Butterworth, 1995). Such behaviors have also been observed prenatally (Zoia et al., 2007).

Core Knowledge about Other People

The third kind of core principles are those that regulate the interaction between individuals. These principles involve understanding the social signals that inform us about other people's emotions and intentions. The social rules and regularities are the most complicated to understand and master. Newborn infants are attracted by faces (Johnson & Morton, 1991) and are sensitive to the direction of gaze of other people (Farroni, Csibra, Simion & Johnson, 2002). Farroni et al. showed that newborn infants look longer at a face with the gaze directed at them than at a face with averted gaze. Furthermore, four-month-olds follow the gaze of a depicted person after a picture of direct gaze has been shown. Newborns also turn their face toward a human voice (Muir & Field, 1979). They perceive and communicate emotions such as pain, hunger, and disgust (Wolff, 1987). Within a few weeks from birth, they smile back toward a smiling face and take turns with a conversation partner (Trevarthen, 1980). These predispositions give social interaction a flying start.

Motives Drive Development

The development of biological organisms depends crucially on motives. Motives precede all actions and are their driving force. They function from birth. The motives of children match their core knowledge dispositions. The knowledge about objects and events corresponds to motives to explore and learn about the surrounding world; the knowledge about one's own movements corresponds to an eagerness to improve and develop one's potentials for action; and the knowledge about other people corresponds

to the child's devotion to social interactions. The motives are not independent of each other but rather intricately interwoven. For instance, the motive to explore depends on the motive to move, and the motive to move depends on the social motive.

Exploring the External World

The explorative motive makes infants develop their knowledge about objects and events around them. Infants are extremely curious of everything that is new and unexplored. They rapidly learn about it. When the objects and events are known, they are much less interesting. This is such a profound characteristic of infant behavior that the most common way of investigating infant cognition is to show an object or event several times to an infant. The children will look less on every new presentation, and when the looking time has decreased to a certain lower level, a change is introduced. If the children are sensitive to this contrast, they will then increase their looking again.

When infants master functional reaching, they spend much time on exploring objects manually. They use both hands to slide, bang, squeeze, wave, tear, rotate, and finger the objects. Observing five- to six-month-olds handle a piece of paper is fascinating (fig. 10.2). They tear, pull, wrinkle, and mouth the paper with persisting energy. It is hard to imagine the full impact of the curiosity motive. In a recent study where 11- and 13-month-olds were video-recorded in their homes for one hour, Karasik, Tamis-LeMonda, and Adolph (2011) found that the infants made contact with about 40 objects during that time, corresponding to a new object every 1.5 minute. The motive to explore objects is closely related to the social motive of the child. Not only do children explore objects and events for their own benefit, but they also want to share their newly acquired knowledge with other people. Karasik et al. (2011) found that in a large majority of the cases, the infants in her study showed the objects to the parent who was present and often carried the objects to them.

Exploring One's Movement Capabilities

Children's motivation to explore their movement capabilities is impressive. Before they master reaching, for instance, they spend hours and hours trying to reach for an object even though they will fail, at least to begin with. They will abandon established patterns of behavior in favor of new ones even when this implies a setback in movement efficiency. For instance, infants stubbornly try to walk at an age when they can locomote much more efficiently by crawling or sliding. In these examples, there is no

Figure 10.2
An infant exploring bimanually a shiny paper in front of her.

obvious external reward. It is as if the infants know that they will be much better off sometime in the future if they can master the new activities. The direct motives are, of course, different. Moving is probably just extremely pleasurable. According to Adolph and Berger (2006), infants who have recently started to walk take, on the average, over 9,000 steps during a day. Expanding one's action capabilities is highly rewarding. When new possibilities open up as a result of, for example, the establishment of new neuronal pathways, improved perception, or biomechanical changes, children are eager to explore them. At the same time, they are eager to explore what objects and events in their surroundings afford in terms of new modes of action (Gibson & Pick, 2000). The pleasure of moving makes children less focused on what is to be achieved and more on their movement possibilities. It makes children try many different procedures and introduces necessary variability into the learning process.

Exploring the Social World

From a very early age, infants find it extremely rewarding to interact with other humans and make other humans enjoy interacting with them. The

social motive puts the infant in a broader context of other humans that provide information, comfort, and security. From other people, children can learn new skills, find out new things about the world, and exchange information through communication. The social motive is so important that some have even suggested that without it a person will stop developing altogether. Research on children who were abandoned and placed in foster care institutions where they experienced only minimal social stimulation demonstrates that they suffer profound delays in cognitive development (Nelson, Furtado, Fox & Zeanah, 2009). Several different attentional mechanisms guide infants to where the critical social information is. For instance, young infants fixate the eyes of other people to a great extent. Hunnius, de Wit, Vrins, and von Hofsten (2011) found that four-month-olds fixated the eyes of pictures of emotional faces over 40 percent of the total dwell time on the face. When having a real face in front of them, they fixate it intensively and take turns with the other person. It has been reported that from birth, infants imitate facial gestures like mouth opening and tongue protrusion (Meltzoff & Moore, 1983; although see also Ray & Heyes, 2011). From early on, emotional gestures evoke reciprocal reactions in young infants. A smile evokes a smile, and an angry expression evokes a distress reaction (Haviland & Lelwica, 1987).

Learning Mechanisms

There are probably several different principles by which new experience can be incorporated with the existing knowledge of a child, and they seem to be optimally geared to the different learning problems outlined earlier.

(a) Statistical learning seems to be optimally geared to learn to differentiate phenomena in the external world. In fact, this is the kind of learning that Gibson (1966) called "learning of higher order variables." When regularities appear in visual patterns (Fiser & Aslin, 2002) or auditory sequences, infants learn those regularities very fast (Saffran, 2003).
(b) The learning involved in the development of new modes of action, like crawling, upright locomotion, reaching, grasping, and manipulation, is reinforcement learning in the sense that feedback provides a basis on which actions can be compared. It is different from externally rewarded learning, however, in that it relies on intrinsic motivation (Barto, 2002; Berthier, Rosenstein & Barto, 2005). Intrinsic motivation refers to being moved to do something because it is inherently enjoyable and leads organisms to engage in exploration and play. The principles of this motive are

in accordance with what is suggested by the novelty response of the dopamine system (Singh, Barto & Chentanez, 2005). It implies that all novel actions have rewarding properties (Singh et al., 2005). Using this principle, children vary their behavior in an exploratory way to discover appropriate ways of acting in different contexts. The model is consistent with what is known about how neural systems evaluate behavior (Schultz, Dayan & Montague, 1997).

(c) It seems that we might learn about other people's actions by projecting them onto our own action programs. The underlying assumption is that the principles that govern other people's actions are the same as those that govern our own. Devoted mechanisms in the brain help the child to take this shortcut to social understanding (the mirror neuron system, or MNS). A number of studies have found evidence that the neural circuits activated when performing actions are also activated when observing the same actions (Fadiga, Fogassi, Pavesi & Rizzolatti, 1995; Rizzolatti & Craighero, 2004; Mukamel, Ekstrom, Kaplan, Iacoboni & Fried, 2010). By projecting other people's actions onto our own action systems, not only the movements themselves become available to us but also the intentions and emotions associated with them.

The Developmental Process

Although perception and action are deeply rooted in phylogeny, they would be of little use if they did not develop. Development is the result of a process with two foci, one in the central nervous system and one in the subject's actions. The brain undoubtedly has its own dynamics that make neurons proliferate, migrate, and differentiate in certain ways and at certain times. However, the emerging action capabilities are also crucially shaped by the subject's interactions with the environment. Perception, cognition, and motivation develop at the interface between neural processes and actions. They are a function of both and arise from the dynamic interaction between the brain, the body, and the outside world. Organized movements of the human child are observable from the ninth week of gestation. Within a month, the fetus will begin to make organized paradoxical breathing movements, open and close the mouth, yawn, suck, and swallow. At 22 weeks of gestation, the hand movements of a fetus are planned in the sense that those directed to the eye are more smooth, decelerated, than the ones toward the mouth (Zoia et al., 2007). Spontaneous neural activity at the retinal level ensures that enough structured

activity at the retina is provided to map up the visual system (Shatz, 1996). It is possible that the spontaneous activities of the fetus also facilitate the mapping of the visuomotor system. Moving the arms in front of the eyes in the womb produces moving shadows over the eyes that might assist in the mapping of the visual system. In addition, the change in the light level when the arms move in front of the eyes provides information about the contingencies between arm movements and visual input.

The brain develops in a most dramatic way during the first year of postnatal life. In fact, it doubles in size. This is due not to any increase in the number of nerve cells but to a massive increase in the connectivity between cells, especially in the cerebral cortex and the cerebellum (Huttenlocher, 1990). This dynamic development results in new forms of perception, action, and cognition (Thelen & Smith, 2003). The emergence of new forms of action always relies on multiple developments. The onset of functional reaching depends, for instance, on differentiated control of the arm and hand, the emergence of improved postural control, precise perception of depth through binocular disparity, perception of motion, control of smooth eye tracking, the development of muscles strong enough to control reaching movements, and a motivation to reach.

Acquiring Knowledge about Events

Perception of Motion

To perceive and predict upcoming events, perception of motion is crucial. It is not clear how well newborn infants perceive motion. It has been reported that they prefer to fixate biological motion patterns when paired with random motion (Simion, Regolin & Bulf, 2008). They were also shown to discriminate between upright and inverted biological motion patterns. This implies that newborns, in certain respects, possess a system for perceiving motions. At the same time, they are bad at tracking objects with smooth pursuit, which is based on perception of directed motion. Kremenitzer, Vaughan, Kurtzberg, and Dowling (1979) found that neonates would smoothly track a 12° black circle, but with low gain and only approximately 15 percent of the time. The answer to this apparent paradox is probably that motion is processed in two different ways early in life. One way is through the subcortical structure of the superior colliculus (Berman & Wurtz, 2010). This is a phylogenetically old structure that might be sensitive to biological motion. The information is then relayed via pulvinar to the occipital-temporal junction (corresponding to middle temporal–middle superior temporal [MT-MST]). It has been found that

cortical motion processing is not located centrally in V1 in young infants but rather located laterally in areas that closely correspond to MT-MST (Wattam-Bell et al., 2010; Rosander, Nyström, Gredebäck & von Hofsten, 2007). Cortical processing of directed motion appears at around two months. Only then does VEP discriminate clearly between motion directions of displayed motion (Wattam-Bell, 1991). At the same age, infants begin to track visual targets with smooth pursuit (von Hofsten & Rosander, 1997).

Smooth pursuit is an important ability for two reasons. First, any velocity difference between the eye movement and the fixated moving object will result in smearing of the object on the retina and a resulting decrease in acuity. Second, as the resolution on the retina decreases rapidly with the eccentricity of the projection, it is crucial to keep the projection of a fixated object on the fovea. The improvement in gain of smooth pursuit over age fits closely with the development of discrimination of motion direction (Atkinson, 2000). Smooth pursuit becomes adultlike at around four months. At that age, infants smoothly track fast-moving objects without a lag. This mode of tracking depends on an internal model of the moving stimulus and combines with head movements in an additive way. The development of smooth pursuit is closely related to the development of the ability to perceive directed motion (von Hofsten, 2004).

At around four months, infants track moving objects over temporary occlusion by making a saccade to the reappearance point before the object reappears there (Rosander & von Hofsten, 2004; von Hofsten, Kochukhova & Rosander, 2007). The smooth-pursuit tracking is typically interrupted by the disappearance of the object, and just before the object reappears, gaze moves to the reappearance position. This timing behavior was demonstrated over a large range of occlusion intervals, suggesting that the infants track the object behind the occluder in their mind's eye. This ability was also found to be strongly correlated ($r = 0.85$) with smooth-pursuit skills (von Hofsten et al., 2007). This is especially interesting because the gaze shift over the occluder is saccadic. Therefore it is not the mode of tracking that unites these two tasks but their predictive nature. They both rely on an ability to anticipate motion. It fits with evidence showing that rhesus monkeys represent the velocity of an object they track in their frontal eye field when it is visible, as well as when it is temporarily occluded (Barborica & Ferrera, 2003).

Acting on the Physical Environment

At around four months, infants begin to successfully grasp objects within reach. When planning a reach, the infant takes the direction and distance

to the object into account, and the hand starts to close before the object is encountered (von Hofsten & Rönnqvist, 1988). A number of other predictive adjustments are also part of the early grasping skills. The hand will adjust its angular posture in anticipation of a rod's inclination (von Hofsten & Fazel-Zandy, 1984) and turn in an anticipatory way when reaching for a turning rod (von Hofsten & Johansson, 2009). The hand will also open more for a large than a small object, and two hands are used if the object is large.

A remarkable ability of infants to time their manual actions relative to an external event is demonstrated in early catching behavior (von Hofsten, 1980, 1983; von Hofsten, Vishton, Spelke, Feng & Rosander, 1998). Von Hofsten (1980) found that infants reached successfully for moving objects at the same age they began mastering reaching for stationary ones. Eighteen-week-old infants were found to catch an object that moved at 30 cm/s. The reaches were aimed toward the meeting point with the object and not toward the position where the object was seen at the beginning of the reach. Eight-month-old infants were able successfully to catch an object that moved at 120 cm/s (von Hofsten, 1983) (fig. 10.3). When reaching for the moving object, infants were shown to extrapolate the motion

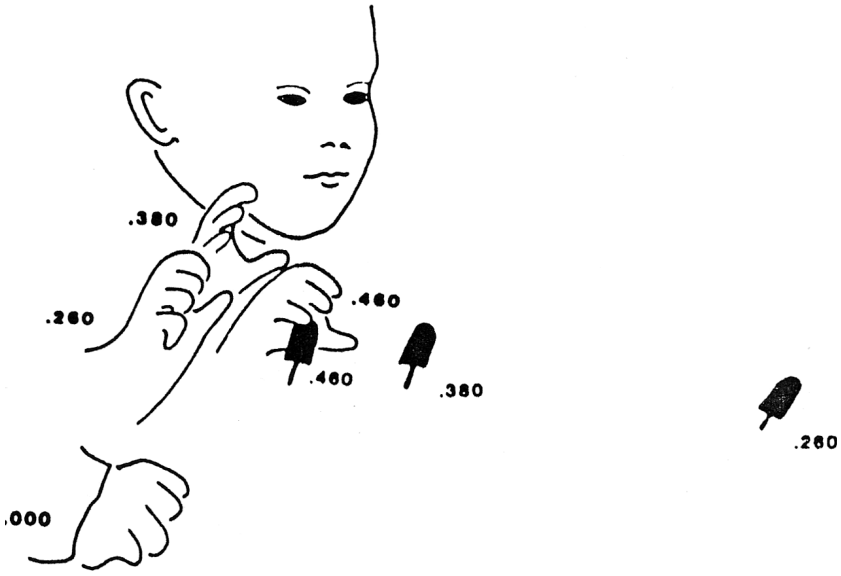

Figure 10.3
An eight-month-old catching an object moving at 120 cm/s. The numbers depict movement times for the hand and corresponding times for the object during the approach. Note that when the hand begins to move, the object is still far outside the picture. From von Hofsten (1983).

trajectory, thereby demonstrating knowledge about the inertia principle. When the trajectory of the object was perturbed 90°, infants would continue to look at and move the hand along the previous trajectory for at least 200 ms (von Hofsten et al., 1998).

Postural Control

As Reed (1996) stated, "Maintenance of posture in the real world involves much more than simply holding part of the body steady; it is maintaining a set of invariant activities while allowing other activities to vary" (p. 88). Gravity gives a basic frame of reference for such orientational stability, and almost all animals have a specialized mechanism for sensing gravity (in humans, this mechanism is the otoliths). Gravity is also a potent force, and when body equilibrium is disturbed, posture quickly becomes uncontrollable. Therefore any reaction to a balance perturbation has to happen extremely fast. For instance, when one slips on a patch of ice, ongoing actions are interrupted, and a series of fast automatic responses is elicited to serve the goal of regaining balance. However, disturbances to balance are better handled in a predictive way, because if the disturbance can be foreseen, one has no need for an emergency reaction, and ongoing actions can continue.

In upright stance, the body acts as a standing pendulum. The natural sway frequency of a pendulum is inversely proportional to the square root of its length. The shorter the child, the higher is the frequency with which it sways. Consequently there is less time to react to balance disturbances. Thus when, at the end of the first year, infants start to be able to stand independently, they have mastered a balance problem more difficult than at any time later in life. In young children, the predictive control of balance becomes extremely important. A nice example of how this mode of control emerges is provided by Barela, Jeka, and Clark (1999). They examined how infants used a handrail to control sway during upright stance. The subject's body sway and the forces applied to the contact surface by the subject were both measured. The youngest subjects applied forces to the contact surface as a physical consequence of their body sway, whereas the oldest infants applied forces to the contact surface in anticipation of body sway.

Reaching perturbs balance. When the subject extends the arms forward, the point of gravity of the whole body is displaced forward, which will push it out of equilibrium if nothing is done about it. Witherington et al. (2002) examined anticipatory postural activity in infants of different ages when they prepared a pulling action. The task required standing infants to open a cabinet drawer to retrieve toys while a force resisting the pulling

action was applied to the drawer. Before each trial, an attractive toy was placed in the drawer to entice the infant to pull it open and retrieve the toy. The proportion of pulls involving anticipatory activity in the gastrocnemius muscles before the pulling action began increased progressively between 10 and 17 months. The emergence of independent walking coincided with marked anticipation. The most substantial increase in anticipatory postural adjustments relative to pull onset occurred between the prewalking infants and the early walkers. Highly specific anticipatory adjustments in the gastrocnemius muscle within 240 ms before pull onset increased from roughly one-third of the pulls to more than one-half.

Manipulation

During the second year of life, children are fascinated by problems of how to relate objects to each other. They put objects into piles, put lids on pans, and insert objects into holes. Such manipulations of objects require sophisticated representation of objects and events. The child must imagine the goal state of the manipulation and the procedures of how to get there. Örnkloo and von Hofsten (2007) studied how children come to master the fitting of objects into apertures. The task was to insert elongated objects with various cross sections (circular, square, rectangular, elliptical, and triangular) into apertures in which they fitted snugly. Although 14- to 18-month-olds understood the task of inserting the blocks into the holes and tried hard to do so, they were not very successful. Most of the time, they did not even orient the longest axis elongated blocks vertically but just put them on the aperture and tried to press them through. The 22-month-old children, however, systematically oriented the horizontally placed objects in a vertical position and turned them appropriately around the vertical axis when transporting them to the aperture. The results show that the infants were successful only when they had prepared the insertion of the objects in this way. Preparing the proper orientation adjustments before inserting the object into the hole requires the child to mentally rotate the manipulated object into the fitting position ahead of time. The ability to imagine objects at different positions and in different orientations greatly improves the children's action capabilities. It enables them to plan actions on objects more efficiently, to relate objects to each other, and plan actions involving more than one object.

Interacting with Other People

An important difference distinguishes social actions from those used for negotiating the physical world. That one's own actions affect the behavior

of the person toward whom they are directed creates a much more dynamic situation than when actions are directed toward objects. Socially relevant information that is important to perceive and control is readily displayed by specific movements, gestures, and sounds. Facial gestures convey information about emotions, intentions, and direction of attention. The development of social perception is facilitated by a set of predispositions that create an optimal learning environment for understanding social interaction.

One important determinant of social perception is the mirror neuron system (MNS) that is activated both by the execution of one's own goal-directed actions and by the perception of someone else performing the same actions (Rizzolatti, Fadiga, Fogassi & Gallese, 1996; Rizzolatti & Craighero, 2004). The goal-directedness of actions has been found to be a critical feature in the activation of mirror neurons (Umiltà et al., 2001; see also chap. 8 in this volume). Recently Mukamel, Ekstrom, Kaplan, Iacoboni, and Fried (2010) found an abundance of mirror neuron cells in human medial frontal and temporal cortices in patients undergoing brain operations. The activity was measured while patients executed or observed hand grasping actions and facial emotional expressions. As these areas are not parts of the traditional MNS areas (area 44/45 and inferior parietal lobule), the researchers concluded that humans may be endowed multiple neural systems for mirroring other people's actions. In fact, mirroring other people's actions may be one of the basic principles of the functioning human brain.

The MNS has important implications for development. As the MNS hypothesis states that other people's actions are understood in terms of one's own action programs, it is expected that observed actions are not understood until subjects master those actions themselves. Thus if the MNS hypothesis is valid, we should expect that the development of children's understanding of other people parallels children's own action development. As infants become more proficient in the action domain, they rapidly develop social skills, requiring knowledge of other people's actions. For instance, from about two months, infants return a smile. We used two ways to evaluate the early functioning of the MNS system.

First we tested the MNS system indirectly by measuring adults' and infants' spontaneous tendency to anticipate the goal of other people's actions when observing them. For the acting person, proactive eye movements to the goal make sense because the actions can then be guided from that position (Johansson, Westling, Bäckström & Flanagan, 2001). What is more remarkable is that subjects in an action observation situation will also make proactive eye movements to the goal (Flanagan & Johansson,

2003), although it does not serve any obvious purpose. However, if other people's actions are understood by projecting them onto one's own action system, predictive looking at the goal in this situation should be expected.

Rosander and von Hofsten (2011) asked whether people's actions are understood by projecting them onto one's own action programs, according to the MNS hypothesis, and whether this mode of control functions in infants. Adults' and 10-month-old infants' hand and gaze movements were measured in two live situations. The task was either to move an object between two places in the visual field or to observe the corresponding action performed by another person. When performing the action, infants and adults behaved in a strikingly similar manner. Hand and gaze movements were simultaneously initiated, and gaze arrived at the goal 400–500 ms ahead of the hand. When observing the actions, the initiation of the gaze shift was delayed relative to the observed hand movement in both infants and adults (250 ms in the adults and 340 ms in the infants), but in both groups gaze still arrived at the goal ahead of the hand. The close similarity between adults' and infants' actions when performing the movements and the great advantage of the adults when observing them suggest that the MNS system is gradually established during development; that is, infants learn relevant actions before being able to match other people's actions to it.

Falck-Ytter, Gredebäck, and von Hofsten (2006) measured how adults, 12-month-olds, and 6-month-olds observed displacement movements. They found that both adults and 12-month-olds shifted gaze proactively to the goal of the observed actions. The 6-month-old infants, however, did not do that. On the contrary, their gaze movements were linked reactively to the course of events. In a control condition where everything was the same as in the original displacement condition except that no hand producing the movement was visible, neither the adults nor the children moved to the goal proactively.

These two experiments suggest that the ability to predict observed displacement movements develops sometime between 6 and 10 months. As the mirror hypothesis states that the observed actions are projected onto one's own motor programs, we should expect that movements not yet mastered by the child should not be mirrored. Six-month-olds do not yet systematically move objects from one position to another. If they pick up an object and displace it, they almost always move it to the mouth. Kochukhova and Gredebäck (2010) measured how six-month-old infants track observed movements to the mouth. They found that six-month-olds shift gaze very proactively to the mouth (lead 0.5 s). When the hand moving the food to the mouth was invisible, gaze arrived at the mouth

after the spoon. These results suggest that the onset of a functional MNS is set by the motor experience of the child. Movements directed at the mouth are understood at an earlier age than movements directed at another point in action space.

The other way in which we studied the onset of a functional MNS was through EEG measurements. The mu rhythm, a specific frequency interval in the EEG spectrum (9–13 Hz in adults and 5–9 Hz in infants), is enhanced during rest and desynchronized during action performance. The same desynchronization appears during the observation of actions in adults (Hari et al., 1998). This has been taken to indicate that the desynchronization of the mu rhythm reflects the activity of the MNS. If this is so, then the desynchronization of the mu rhythm should be greater when subjects observe goal-directed movements than when they observe movements that do not have obvious goals. Recently Nyström, Ljunghammar, Rosander, and von Hofsten (2011) found that eight-month-old infants who observed live goal-directed reaching actions showed a greater desynchronization of the mu rhythm than when they observed simple placing movements of the hand performed by the model. The reaching and the placing movements were similar in the sense that both transported the hand to a tabletop. Furthermore, the EEG analysis showed that it was primarily the electrodes over the premotor areas that showed this effect. This area is known to be important for the functioning of the MNS (Rizzolatti & Craighero, 2004). In a similar study, Southgate, Johnson, Karoui, and Csibra (2010) found that the mu rhythm in nine-month-olds was attenuated both when the children themselves performed reaching movements and when they observed someone else performing them.

In summary, both the EEG studies and the studies of predictive eye movements suggest that the MNS related to manual actions becomes functional during the second half of the first year of life. As infants come to master their own manual actions, they also begin to understand such actions performed by other people. The studies support the hypothesis that this knowledge is mediated by a devoted neural system anchored in the subject's own motor system.

Conclusion

Cognitive development cannot be understood in isolation. It is related to the motives of the child, the action problems to be solved, and the constraints and possibilities of the child's body and sensory-motor system. By necessity, action control relies on anticipation of what is going to happen

next, and this is based on knowledge of the rules and regularities that govern events. The ability to coordinate one's actions with the dynamic physical and social world reflects perceptual and cognitive systems that foresee what is going to happen next. With little experience, infants track objects predictively with their eyes and catch fast-moving ones.

Being in charge requires not just anticipating physical events but also anticipating social events and relating one's own actions to the actions of other people. Recent research shows that specific areas in the brain encode our own and other people's actions alike, and this forms a base for understanding how the actions of others are carried out, as well as the goals and motives that drive them. These facts argue for devoted systems in the brain that provide immediate knowledge of the world. They are anchored in the child's own action systems.

Piaget (1953, 1954) realized that an important ontogenetic connection exists between action and cognition, but he postulated that this connection fades with the onset of rule-based thinking. It is obvious that the link between action and cognition may seem less direct in older children and adults because they can simulate events and their outcomes in their minds. This does not mean, however, that the rules that govern these processes are different from those that govern actions more directly. On the contrary, in both infants and adults, actions are fitted to the flow of events that occur around them. There is no time for contemplation. The subject must realize what is going to happen next and be prepared to act.

Acknowledgments

This chapter was made possible by support to the author from the Norwegian Directorate for Children, Youth, and Family Affairs (06/34707).

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11 Developmental Perspectives on Action Science: Lessons from Infant Imitation and Cognitive Neuroscience

Andrew N. Meltzoff, Rebecca A. Williamson, and Peter J. Marshall

Introduction

Before Silicon Valley became known for computers and Stanford University, the region spawned innovations in action science. In 1882 the politician Leland Stanford asked the photographer Eadweard Muybridge to investigate a puzzle in biomechanics: do all four hooves of a galloping horse leave the ground at the same time? Muybridge's photographs showed that galloping horses were momentarily airborne, settling the dispute about "unsupported transit."

Muybridge was obsessed with action. In *Descriptive Zoopraxography, or The Science of Animal Locomotion* (1893), Muybridge developed technology that was the forerunner of today's motion pictures. In *The Human Figure in Motion* (1901), he provided a "dictionary of human action." The history of developmental psychology and action science might have been different if Muybridge had turned his genius to documenting action learning and development.

Thirty years after Muybridge, Jean Piaget began his classic studies of action from a developmental perspective. Piaget's theory of cognitive development was built on two pillars: the action assumption and the invisibility assumption. The action assumption holds that all knowledge is rooted in action, and the two are inseparable in infancy: to know an object is to use it, and the acquisition of new knowledge requires motor exploration. Preverbal infants are confined to "knowing how," not "knowing that." The corollary, the invisibility assumption, proposes that when young infants lose sensory and motor contact with an object, the object ceases to exist for them (the Piagetian problem of "object permanence").

Modern developmental scientists have reexamined Piaget's theory of infant action and cognition. Using the technology spawned by Muybridge (digital video-recordings), there is now an emerging developmental science

of action. This field examines many of the phenomena highlighted by Piaget: reaching and grasping, play, and imitation. Although contemporary developmental science shares Piaget's conviction that action is central to infancy, the prevailing ideas are no longer strictly Piagetian. Nowhere is this more evident than in the topic of the imitation of action.

Piaget defined imitation in a commonsense way: one person reproducing the acts of another. A problem, however, is that such duplication may occur by chance. We adopt a more technical definition following Meltzoff (2005): "Imitation occurs when three conditions are met: (a) the observer produces behavior similar to that of the model, (b) the perception of an act causes the observer's response, and (c) the equivalence between the acts of self and other plays a role in generating the response." Equivalence need not be registered at a conscious level, but if it is not used at any level in the system (neurally, cognitively, computationally), it is judicious to describe the behavioral correspondence using some other term than "imitation."

This chapter provides a developmental perspective on action representation, using imitation as a focal point. The study of imitation is a burgeoning area and has attracted interest from diverse interdisciplinary fields including developmental science, experimental psychology, cognitive neuroscience, robotics, evolutionary biology, and the philosophy of action (e.g., Dautenhahn & Nehaniv, 2002; Hurley & Chater, 2005; Meltzoff & Prinz, 2002; Meltzoff, Kuhl, Movellan & Sejnowski, 2009). The study of imitation helps to elucidate the psychological and neural mechanisms connecting action perception and production and sheds light on the social-cognitive functions and consequences of such connectivity.

We consider seven interrelated themes. First, we analyze Piaget's view of action development with respect to imitation. Second, we review discoveries about neonatal imitation and deferred imitation (imitation from memory). The theory is developed that humans, starting from infancy, have a "supramodal representation" of human action that undergirds imitation. Third, we show that children's imitation is not rote but flexible and selective in surprising ways. Fourth, we discuss young children's ability to reenact inferred goals, rules, and strategies underlying visible behavior. Fifth, we review studies demonstrating that action imitation is not an uncontrollable impulse but can be regulated by top-down control. Sixth, we highlight that young children are emotionally engaged by being imitated. The mechanisms involved in imitation are bidirectional, supporting both the generation of imitative action and the recognition of being imitated by others, with deep consequences for social development. Finally, we consider imitation from a neuroscience viewpoint. There is interest

in how to connect behavioral imitation to the work on neural mirroring systems. We examine potential links and also discuss pitfalls in overinterpretations. The most relevant neuroscience work in infants derives from newly emerging studies using the electroencephalogram (EEG), with a focus on developmental aspects of the mu rhythm, and we analyze these studies.

Piaget's Stages of Imitation as Windows into Action Development

Piaget's (1962) theory postulates six stages of action imitation between 0 and 24 months of age, which can be grouped into three broader levels.

At level 1 (0–12 months, encompassing stages 1–3) infants are thought to be restricted to imitating simple vocal and manual maneuvers such as hand opening or finger movements. The key to such imitation, according to Piaget, is that infants can perceive both the adult's model and their own responses through the same perceptual modality. For example, manual imitation can be guided visually through within-modality pattern matching. The adult's acts can be compared directly or "assimilated" to the infant's.

At level 2 (12–18 months, encompassing stages 4–5) infants go beyond within-modality comparisons. The landmark development in level 2 is the imitation of facial gestures at approximately one year. Although the infant can see an adult's face, he cannot see his own. Piaget referred to facial imitation as "invisible imitation" and regarded it as a sophisticated achievement drawing on cognitive resources that are not available to younger infants.

At level 3 (18–24 months, encompassing stage 6) infants first become capable of "deferred imitation," that is, imitation from memory. According to Piaget, deferred imitation emerges synchronously with other complex cognitive abilities such as symbolic play, insightful problem solving, and high-level object permanence.

Theoretical Challenge Posed by Facial Imitation: Implications for Action Science

Piaget's theory of cognitive development dominated developmental science for 50 years. Research using experimental methods has emerged to test his predictions, which were based on case studies of his own three children. This newer research does not support the stagelike emergence of action imitation that Piaget envisioned.

A significant piece of evidence against Piaget's stage-developmental model comes from studies with human neonates. Meltzoff and Moore

(1977) reported that 12- to 21-day-old infants were able to imitate facial gestures such as tongue protrusion. Although the results first came as a surprise, the findings have now been replicated in more than two dozen experiments (Meltzoff & Moore, 1997). Researchers are now exploring the psychological and neural mechanisms underlying this behavior and the functions that imitation serves.

Ruling Out Alternative Explanations for Neonatal Imitation

Crucial controls were included in the tests of early facial imitation to exclude low-level explanations. One concern is that infants might be more aroused when they see an adult act, and therefore increase their general activity, including their facial movements. The specificity of the responses rules out this explanation. Infants respond differentially when the same face, at the same distance, moving at the same rate, performs two closely matched gestures (e.g., tongue protrusion versus lip protrusion). Moreover, studies since 1977 have shown that infants differently imitate two different types of tongue protrusion—ordinary tongue protrusion versus tongue protrusion to the side (Meltzoff & Moore, 1994, 1997). An arousal interpretation cannot account for such response specificity. Nor can arousal account for the range of gestures that have been documented, including lip, tongue, head, and manual actions (see Meltzoff & Moore, 1997, for a review).

What about associative learning? Might infants learn to associate the oral movements they see with their own oral movements through experience with feeding or parental imitation of the children's own behavior? Piaget carefully analyzed associationism as an account of imitation and identified several logical and empirical shortcomings of this view.[1] As a more direct test, Meltzoff and Moore conducted two studies using newborns who were still in the hospital after birth. One study found imitation of mouth opening and tongue protrusion (Meltzoff & Moore, 1983); the other found imitation of head movements (Meltzoff & Moore, 1989). The mean age of the participants in these studies was 36 hours old; the youngest was only 42 minutes old. This renders associative learning induced by adult imitation of the child an unlikely basis. Of course, associative learning may occur in older infants, but it is not a necessary precursor for imitation to occur in the first place.

Temporal Flexibility and Response Correction: Evidence for a Closed-Loop System

If arousal and learned associations cannot account for the early matching responses, what other explanatory mechanisms can we turn to, and what

are the implications for action science? One possibility is rooted in Gibson's theory of perceptual-motor resonance. Gibson (1966, 1979) developed the notion of resonance, drawing on the analogy of two tuning forks. Meltzoff and Moore (1977) wondered whether neonatal imitation might be explained by such Gibsonian resonance. This led to an experiment in which neonates had a pacifier in their mouths while observing an adult's action. After the infant observed the adult action, the adult stopped gesturing, assumed a passive face, and only then removed the pacifier. Despite having direct resonance blocked by the pacifier—even engaging in alternative activity (sucking)—infants imitated (Meltzoff & Moore, 1977, experiment 2). Subsequent studies also reported temporal gaps between the stimulus and the response (Fontaine, 1984; Heimann, Nelson & Schaller, 1989; Heimann & Schaller, 1985; Legerstee, 1991; Meltzoff & Moore, 1994). Matching through perceptual resonance probably occurs in infants and adults, but neither is restricted to it.

Beyond the raw existence of early imitation, the most important discovery for action science concerns the organization of the response. Empirical evidence from several independent laboratories shows that the infants' first imitative responses are not complete reproductions of the adult's (Abravanel & Sigafoos, 1984; Heimann, Nelson & Schaller, 1989; Meltzoff & Moore, 1977, 1983). A microanalysis of the response reveals that infants gradually correct their imitative attempts over time in a sequence of ordered steps (Meltzoff & Moore, 1994). Our interpretation is that infant imitation is organized by the goal of matching the adult's target, which is compatible with other findings of primitive goal-directedness in the actions of infants (Butterworth & Hopkins, 1988; von Hofsten, 2007).

A Psychological Mechanism for Imitation: AIM Hypothesis and Body Babbling

Meltzoff and Moore (1977, 1997) proposed that imitation is based on active intermodal mapping (AIM). The core idea is that infant imitation is rooted in infants' capacity to register equivalences between the bodily transformations performed by others and the body transformations the infants feel themselves make. In this account, facial imitation involves cross-modal equivalences. The infants' own facial gestures are invisible to them, but they are not unperceived: infants monitor their unseen motor acts through proprioception. Meltzoff and Moore postulated that infants link perception and production through a "supramodal" coding of human acts. This may explain why infants can correct their imitative movements and imitate

from memory: infants store a representation of the adult's act and recursively compare their own imitative efforts against this stored representation. That is what we mean when we say that early imitation involves an "active" component (AIM) and is goal directed.

Body Babbling and Self-Experience

We argue that infants' own motor experience plays a role in early facial imitation. Films of fetal behavior reveal repeated lip, tongue, and hand movements *in utero* (e.g., de Vries, Visser & Prechtl, 1985; Zoia et al., 2007). This self-generated activity continues after birth. Meltzoff and Moore (1997) characterized these movements as "body babbling" and proposed that such motor activity plays a role in action imitation, analogous to the role that vocal babbling plays in speech production (Kuhl & Meltzoff, 1982, 1996).

Tongues move in certain ways, and these ways are very different from the action patterns of hinged joints such as in fingers and elbows. Based on self-experience with the felt movements of one's own body, the kinetic signatures of another person's tongue protrusion and withdrawal (or mouth opening and closing, or finger flexing) could be recognized as cross-modally equivalent to those produced by oneself. A more detailed computational model specifying the "metric of equivalence" that infants use to achieve facial imitation is described elsewhere (Meltzoff & Moore, 1997). This model provides our explanation of what is sometimes referred to as the "correspondence problem" (how the imitator matches perception and production).

Characterizing the Supramodal Action System: Differentiating My Acts from Yours

The ideas about a supramodal representation of human action can be developed further, and a critical point concerns the differentiation between actions performed by the self and observed in others. One possibility might be that the supramodal system is simply a translation device for turning visual perceptions into motor output: a perception-production transducer. There are three reasons to think that we need a more differentiated notion than this, both in adults and in preverbal infants.

First, the observed actions can be remembered and imitated at a later time (the temporal gap studies). These findings suggest that there is a stored representation of the observed act, which allows infants (and adults) to imitate after a temporal delay and after performing intervening motor activity. Second, the imitative acts are corrected to achieve a more faithful

match, and this correction can occur after the demonstration of the target act has stopped and is no longer visible. Thus information from one's acts must be available for comparison to the stored representation of the target act. Third, infants show interest in being imitated themselves, and they recognize when their facial and manual behavior is being copied. Such recognition implies that infants store a representation of their own bodily actions (even if those actions are invisible to them).

Taken together, these three facts suggest a differentiation in the supramodal system. The representation derived from observing the other person's actions is separable from the representation of one's own bodily actions. Successful imitation involves comparing the two. Theories that suppose no distinction—a merging or lack of differentiation between the actions of self and other—cannot easily account for these facts (for further analysis of the mechanism of imitation, see Meltzoff & Moore, 1997, pp. 185–187).

Learning and Memory for Actions on Objects: Instrumental Imitation

Over and above the imitation of gestures, human beings imitate acts they see others perform on objects. Before language becomes available to the child, imitation is a chief mechanism by which they learn about tool use and acquire causal knowledge about how novel objects and machines work. This "instrumental imitation" continues to play such a role in adults: how to tie a knot, build a fire, or use a lever is more efficiently learned through studying others' behavior than via an instruction manual or a linguistic narrative.

In imitation involving objects, immediate responding is often not possible. There may be only one object, and the child may not have access to it during the time that the expert is demonstrating what to do. Children often watch adults' object manipulations and imitate at a later time when granted access to the object or tool. Such "deferred imitation" goes beyond immediate perception-production coupling and constitutes an important aspect of human learning. From the point of view of action science, deferred imitation also provides a way of exploring the memory and representation of action.

In using deferred imitation to investigate memory for actions, it is crucial to distinguish between (a) forming a representation of an act from observation alone, and (b) retaining one's own already executed behavior (or motor habit) over time. At stake is whether an action has to have been initially executed to be retained over long intervals.

This distinction has been addressed using the "observation only" design in deferred imitation (Meltzoff, 1995b). In this design, children are shown target acts on objects but are not allowed to touch or handle the objects. After a delay, children are allowed to manipulate the objects for the first time. Control groups are used to evaluate the spontaneous manipulations of children at this age. Infants in the second year succeed in imitating after delays as long as four months using the observation-only procedure (Meltzoff, 1995b). Deferred imitation of actions on objects has been documented in infants as young as 6 to 12 months (Barr, Dowden & Hayne, 1996; Klein & Meltzoff, 1999; Meltzoff, 1988b), which runs against the Piagetian stage-developmental model.

Importantly, infants can also perform deferred imitation of completely novel acts on objects. In one experiment, Meltzoff (1988a) discovered that infants would imitate a novel act such as leaning forward to touch a box with their forehead so as to turn on a light. The experiment was set up so that the infants carefully observed the novel act without distractions. After a one-week delay, infants were presented again with the box, and the results showed successful imitation of the head-touch act. These results are based on imitation, because the object's properties alone did not elicit the response in control infants (who were given the box but did not see the relevant action demonstration). Such deferred imitation using the observation-only design established that infants can generate a novel act based on a stored memory of a perceptually absent act they saw in the past.

The organization of the deferred response illuminates issues about action representation. The deferred-imitation response is not a trial-and-error process in which children run through a variety of acts, eventually recognizing the one that was used with a particular object. The target act is essentially the *first* act that infants do with the object after the delay (Meltzoff, 1988a). Infants rarely confused which act to perform on an object despite having seen a series of different acts on a variety of objects. This accuracy suggests an object-organized representational system. Infants do not represent the observed actions alone; the stored representation includes the object together with the act performed on it.

Outcomes, Hierarchies, Causal Results, and Overimitation

As we have seen, young children imitate actions without objects, such as facial gestures, and they also imitate object manipulations that are more instrumental in nature. This has led researchers to compare the two. Several studies have shown that young children are more likely to imitate behav-

iors that cause salient physical outcomes than behaviors that do not (e.g., body movements alone) (Brugger, Lariviere, Mumme & Bushnell, 2007; Hauf, Elsner & Aschersleben, 2004). Young children also take into account the adult's success in attaining a goal in determining whether and what to imitate (Meltzoff, 2007b; Nielsen, 2006; Schulz, Hooppell & Jenkins, 2008; Want & Harris, 2001; Williamson & Meltzoff, 2011; Williamson, Meltzoff & Markman, 2008).

Bekkering, Wohlschläger, and Gattis (2000) noted that children selectively imitate different aspects of what they see, and proposed that this may be due to their representing actions in terms of a hierarchy of goals. When presented actions to imitate, three- and five-year-olds reproduce those that are highest in the hierarchy. In one study, children saw an adult reach either cross-laterally (across the body) or ipsilaterally (with the arm on the same side of the body). When the adult's reach was directed at a spot on the table (Wohlschläger, Gattis & Bekkering, 2003) or at the adult's own ear (Gleissner, Meltzoff & Bekkering, 2000), children disregarded the manner of reach used and simply reached for the appropriate spot. However, when there was no obvious goal (e.g., when the same hand movement was made but there was no spot), children were more likely to reproduce the exact type of reach with high fidelity. Thus children vary what aspect of the display they imitate depending on what they identify to be the purpose of the behavior (see also Carpenter, Call & Tomasello, 2005; Loucks & Metzoff, in press).

Williamson & Markman (2006) tested a similar idea. Three-year-olds saw an adult place an object using unusual means (e.g., turning a cup over and rotating it in a two-handed grip). When there was no contextual support for this placement, children reproduced the adult's actions with great fidelity; when a context provided the reason for the placement (e.g., the cup was a nose in a face configuration), children imitated the placement but often ignored the precise movements and manner by which the adult put the object there.

Children seem to use a trade-off between reenacting the goal versus the particular actions the adult uses. If children lack a clear understanding of an overall goal or how to achieve it, it is often beneficial for children to imitate the bodily actions in more precise detail. If you imitate the details of the act with fidelity, then the outcome often comes for free—so when in doubt, imitate what the expert is doing and precisely how he or she does it.

This may partially explain a phenomenon that has been termed "over-imitation," the reproduction of actions that are not needed (from the adult's viewpoint) to reach an outcome (e.g., Horner & Whiten, 2005;

Lyons, Young & Keil, 2007; McGuigan, Whiten, Flynn & Horner, 2007; Nielsen & Tomaselli, 2010). In most studies reporting this effect, children reproduce acts that are salient and obviously purposeful by the adult (even if they are causally unnecessary), such as repeatedly banging a handle within a box. Children in these studies may be have doubts about what actions are causally necessary to achieve the demonstrated outcome.

It would be a mistake, we think, to infer from these studies that young children's imitation is always compulsive, rote, or slavish. Evidence suggests that children and adults are flexible and selective imitators who weigh information about the observed outcomes and their understanding of how to achieve them. If children understand how to use an object to reach a desired outcome (e.g., how to use object x to push object y to achieve z), they may choose to reach the same outcome (achieve z) using actions that are easier for them. If, however, they do not understand how to achieve the demonstrated outcome, or if they construe matching the adult's intentional behaviors as a goal in itself, children imitate the precise bodily actions they see with greater fidelity.

Action Interpretation and Inference: Abstracting beyond the Surface Actions

For adults, actions are not processed solely in terms of surface characteristics. Human acts also carry information about something deeper. The envelope of human actions, even the unsuccessful attempts, sometimes reveals information about the actor, including goals and intentions. Several lines of research have begun to explore young children's ability to decode human actions in this way.

Inferred Goals

Human beings are imperfect—we sometimes act in ways we do not intend. We slip; we make mistakes. These mishaps carry information about the actor and his or her goals. The behavioral reenactment procedure was designed to provide a nonverbal technique for exploring goal understanding in preverbal infants (Meltzoff, 1995a). The experimental procedure involves showing infants an unsuccessful act. For example, the adult accidentally overshoots his target, or he tries to pull apart a dumbbell-shaped toy, but his hand slips off the ends and he is unsuccessful. Thus the goal state is not achieved. The experimental question is whether children read through the literal body movements to the underlying goal of the act.

Results show that 18-month-old infants understand the goals the adult is striving to attain, even if these goals are not reached (Meltzoff, 1995a).

Infants who saw unsuccessful attempts at performing an act, and infants who saw the full act, both produced the successful goal-directed target acts at a significantly higher rate than controls (who saw the adult manipulate the object in other ways). Evidently toddlers can extract goals from the envelope of actions that unfold, even without seeing them achieved (see also Bellagamba & Tomasello, 1999; Nielsen, 2009). This interpretation is also supported by infant studies using looking-time methods (e.g., Brandone & Wellman, 2009; Gergely, 2011; Woodward, 1998) and other imitation tasks (Carpenter, Akhtar & Tomasello, 1998; Tomasello & Barton, 1994).

Abstracting Rules and Strategies from Others' Behaviors

Another inference that adults make from seeing actions concerns the rules or strategies that govern the person's behavior. We might not imitate the precise details of another's actions but instead extract and adopt the rules they follow. One important activity used in everyday life and scientific endeavors involves the categorization of objects. People often embody categorization through a set of particular actions, sorting behavior, by which they separate objects into distinct piles according to their properties.

Work by Williamson, Jaswal, and Meltzoff (2010) investigated whether 36-month-olds could learn different categorization strategies by watching the sorting behavior of another person. Children watched an adult sort objects. In one study, the adult sorted according to a visible property (color rather than shape). In a second study, she sorted by an invisible property (sounds made when shaken). In control groups, the experimenter presented a presorted array. Children who saw the adult sorting action sorted the objects (by color or sound) significantly more often than did the controls.

This illustrates the power of imitation. Children can abstract from actions the underlying rules and strategies that generated them, and then can adopt those same rules to generate their own behavior. Based on these inferences, children begin to act like the others in their culture, for example, categorizing an array of objects along the same properties as done by an expert or acting in accord with the roles and cultural norms specified by society.

Top-Down Control of Imitation

Children do not imitate compulsively or blindly; imitation has its reasons. Recent laboratory work has uncovered several top-down influences on imitation.

Social Communication, Naive Pedagogy, and Emotions

Older theories supposed that imitation was automatic, compulsory, and not subject to voluntary choice and control. Increasing evidence indicates, however, that even preverbal children regulate their imitation. In the simplest example, infants are more likely to imitate the actions of a model who engages them socially (Brugger, Lariviere, Mumme & Bushnell, 2007; Nielsen, 2006). Other studies suggest that the "mere belief" that a social agent caused an outcome yields an increase in infants' tendency to imitate it (Meltzoff, 2007b, experiment 3; see also Bonawitz et al., 2010; Meltzoff, Waismeyer & Gopnik, 2012; Thompson & Russell, 2004).

Csibra and Gergely (2006; Gergely, 2011) have suggested that multiple cues, including eye contact and "motherese" intonational patterns, set up an expectation of a pedagogical exchange. Such social cues may draw attention to the relevant aspect of the adult's demonstration and mark it as significant, thus changing the likelihood that it will be chosen for imitation (cf. Gergely, Bekkering & Király, 2002; Paulus, Hunnius, Vissers & Bekkering, 2011; Zmyj, Daum, Prinz & Aschersleben, 2007).

The emotional response that a person gives to an action also serves as a top-down controller of imitation. In one study, an adult performed a seemingly innocent act, and a second adult reacted with negative emotion (saying, "That is so irritating!") as if it were a "forbidden action." The experiment systematically manipulated whether the second adult was looking at the child when the child had a chance to imitate. Children did not imitate the forbidden action if the previously angry adult (now with a neutral face) was watching the child. If the previously angry adult left the room and could no longer visually monitor the child's action, the child would imitate (Repacholi & Meltzoff, 2007; Repacholi, Meltzoff & Olsen, 2008). This documents top-down regulation of imitation based on the expected emotional consequences of performing the action oneself.

Self-Experience

Another line of work shows that children regulate their imitation of actions depending on their own prior action experience. Williamson, Meltzoff, and Markman (2008) tested 36-month-old children to see if they were more likely to imitate another person's actions if the child's own previous experience had revealed that the task was difficult. A surreptitious resistance device made a drawer difficult to open when the child first explored it. Then the adult demonstrated a distinctive technique for opening the drawer (pressing a button on the side of the box). Children were significantly more likely to imitate the adult's distinctive act if the child had a

prior difficult experience with the task. These results fit with educational philosophies asserting that self-experience confronting a problem can help the student be more open to instruction (see also Williamson & Meltzoff, 2011).

Being Imitated: Social-Emotional Consequences

Parent-child games are often reciprocal in nature, and mirroring games are a childhood favorite. What makes a child so engaged and joyful at seeing his or her own actions mirrored by an adult? Temporal contingencies are important, but so is the similarity of the *form* of the participants' actions. Research has investigated whether infants simply prefer people who are acting "just *when* they act" (temporal contingency) or whether they also prefer those who are acting "just *like* they act" (structural congruence).

To test this idea, Meltzoff (2007a) had infants sit across a table from two adults. Both adults sat passively until the infant performed one of the target actions on a predetermined list. Then both experimenters began to act in unison, but one of the adults matched the infant, while the other performed a mismatching response. The results showed that the infants looked and smiled more at the matching adult. This shows that infants are sensitive to the matching *form* of the behavior.

From a cognitive viewpoint, these findings are important because they show that the mechanisms underlying imitation are bidirectional. The machinery that takes visual input and generates a matching motor response can also run in reverse and recognize when the self's own actions are being mirrored.

From a social-emotional viewpoint, the findings are important because they show a social function of imitation. This research revealed that infants are visually engaged by, and have strong positive emotions toward, being imitated by someone else: infants smiled more at the imitator. Being imitated provides a nonverbal bond between the two actors, which may increase emotional attachment, prosocial feelings, and a sense of being understood. Adults also have positive reactions to being imitated even when they are unaware of it (Chartrand & Bargh, 1999). A special "psychological jolt" is induced by seeing one's actions mirrored. Researchers have only just begun to perform the relevant neuroscience studies on being imitated by another person. Work in this area has been carried out with adults (Decety, Chaminade, Grèzes & Meltzoff, 2002) and more recently with infants (Saby, Marshall & Meltzoff, 2012). In both cases, specific neural signatures were found for being imitated by another person.

Cognitive Neuroscience and Action Science

A comprehensive, contemporary action science requires an integration of behavioral findings, cognitive theorizing, and neuroscience data. Much of the neuroscientific study of perception-action coordination has been driven by the concept of the mirror neuron system (MNS). This originates in the discovery, using single-cell recording techniques, of neurons in the ventral premotor cortex (F5) of macaque monkeys that respond not only when a monkey carries out a particular action on an object but also when the monkey observes the same action being carried out (di Pellegrino, Fadiga, Fogassi, Gallese & Rizzolatti, 1992; Rizzolatti, Fadiga, Gallese & Fogassi, 1996).

Although a good deal of evidence exists for overlaps in patterns of regional brain activity between action perception and action production in human adults (Caspers, Zilles, Laird & Eickhoff, 2010; Hari & Kujala, 2009), researchers debate the function of this overlap and its relation to the macaque MNS. We do not aim to address these controversies here. Instead we focus on developmental issues, which have sometimes been overlooked. The corpus of behavioral work on infant imitation firmly establishes that young children link action perception and production. We can infer that some (as yet unspecified) neural circuitry supports such observation-execution coordination. A pressing question is how best to characterize the origins and development of these neural processes (Marshall & Meltzoff, 2011).

EEG as a Tool in Action Science in Adults

The developmental neuroscience work on action processing has mainly employed the electroencephalogram (EEG), with a focus on the sensorimotor mu rhythm. To understand this work, it is first useful to consider results from adult studies. In adults, the mu rhythm occurs in the alpha frequency range (8–13 Hz) and is typically recorded from central electrode sites overlying motor and somatosensory cortices. Early work showed a desynchronization (reduction in amplitude) of the mu rhythm during movement (Gastaut, Dongier & Courtois, 1954), with more recent work examining the specific time course of mu activity during voluntary actions (Pfurtscheller & Lopes da Silva, 1999). Building on recent magnetoencephalography (MEG) findings (Hari et al., 1998), studies with adults have further shown that the mu rhythm is also desynchronized during the observation of others' actions (e.g., Muthukumaraswamy & Johnson, 2004; Streltsova, Berchio, Gallese & Umiltà, 2010). Taken together, these findings raise the

suggestion that the mu rhythm may be informative in the study of neural mirroring mechanisms (Pineda, 2005).

Mu Rhythm and Action Processing in Infancy

There is an explosion of interest in elucidating the properties of the mu rhythm in infancy (for a review, see Marshall & Meltzoff, 2011). A number of studies of the infant mu rhythm in relation to action processing have restricted their testing only to action observation conditions, without including action production conditions (Nyström, 2008; Nyström, Ljunghammar, Rosander & von Hofsten, 2011; Reid, Striano & Iacoboni, 2011; van Elk, van Schie, Hunnius, Vesper & Bekkering, 2008). These studies provided useful information, although without an action production condition, the implications for mirroring processes remain limited.

Two teams have used infant EEG to examine perception-production overlaps more directly. Southgate, Johnson, Osborne, and Csibra (2009) examined EEG responses in nine-month-olds who were reaching for and grasping a small toy. Relative to a baseline epoch, there was a significant desynchronization in the alpha frequency range at central-parietal sites during the infants' reaches. Power in a similar frequency range was also found to be reduced relative to baseline when infants viewed a human hand reaching for and grasping an object. In a second study of nine-month-olds, EEG desynchronization was found in response to a reaching hand in a grasping posture even when the outcome of the hand action was not seen (Southgate, Johnson, El Karoui & Csibra, 2010). This finding was seen as reflecting infants' prediction of the motor program that would be needed to achieve the goal of the action, that is, grasping (see also Csibra, 2007).

Marshall, Young, and Meltzoff (2011) used a different interactive task to examine infants' EEG responses during both action perception and action production conditions. Fourteen-month-old infants took turns with an adult executing and observing a discrete goal-directed act, namely, a button press on a custom-made button box (fig. 11.1). EEG reactivity was examined to both perception and production of the button press, relative to baseline epochs preceding each trial. The study predicted reactivity of the infant mu rhythm (6–9 Hz) over central electrode sites (Marshall, Bar-Haim & Fox, 2002), although it also analyzed activity over a range of other scalp regions.

As predicted, infants' own actions on the button box were associated with a significant desynchronization over the central region. A significant desynchronization also occurred in the same frequency range at central

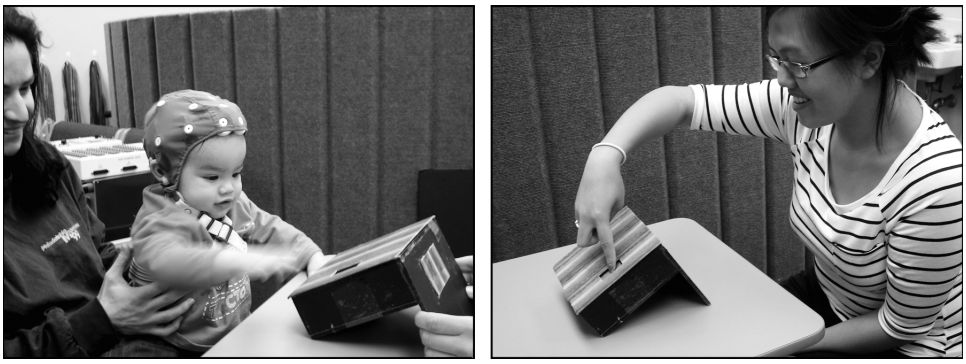

Figure 11.1
Photographs illustrating the execution (*left*) and observation (*right*) conditions in the infant EEG study by Marshall, Young & Meltzoff (2011). Reprinted with permission from Marshall and Meltzoff (2011).

sites when infants simply observed an adult perform the same act. Although the desynchronization during action observation went beyond central sites (to frontal and parietal regions), the desynchronization during action production was more specific to central sites, consistent with work on the adult mu rhythm (Muthukumaraswamy & Johnson, 2004).

Toward a Developmental Neuroscience of Action Processing

The emerging literature on infant EEG suggests that the mu rhythm has utility in the study of the neural processes involved in infants' action processing. It may be tempting to see the infant mu response as a measure of a mirroring mechanism; however, we should be cautious, because research in this area is still at a very early stage. Marshall and Meltzoff (2011) articulated several key questions about the infant mu rhythm that may help to build a firmer foundation for neuroscientific aspects of developmental action science.

One issue concerns the developmental changes that may occur in the mu rhythm (e.g., Berchicci et al., 2011). Another concerns the relative lack of specificity of the EEG response, such that we cannot assume that regional overlaps in desynchronization between conditions necessarily reflect activation of the same underlying neural systems. Infant MEG technologies promise to provide more specific information on regional changes in cortical activity (Imada et al., 2006; Kuhl, 2010).

Another key theoretical issue about mirroring mechanisms is what aspects of perceived actions might be "mirrored" and how such a system

can be related to the demonstrated flexibility of human imitation and action understanding. This question is the subject of much debate in the adult literature (Csibra, 2007; Jacob, 2008; Kilner, 2011; Rizzolatti & Sinigaglia, 2010) but has been less considered from a developmental perspective. Part of this debate concerns the degree to which neural mirroring mechanisms are responsive to the goals of observed actions versus the specific means used. For instance, one unaddressed question concerns whether the mu response in infants is equally responsive to observing actions in which different movements are used to achieve the same goal. At the behavioral level, we know from studies of imitation that infants can imitate both the specific means used and the goal achieved, but the relevant studies have not been conducted using neuroscience measures.

A related theoretical issue concerns top-down influences and the degree to which neural mirroring mechanisms are influenced by social, cognitive, and contextual factors. As we have seen, behavioral studies have documented the flexibility and top-down control of imitation in infants and children.

A final, far-reaching theoretical question revolves around the role of self-experience with actions that an individual observes being performed by others. In adults, various methods have been used to explore self-experience, including experimental psychology (Schütz-Bosbach & Prinz, 2007) and neuroscience (e.g., Calvo-Merino, Grèzes, Glaser, Passingham & Haggard, 2006; Marshall, Bouquet, Shipley & Young, 2009). From a developmental perspective, work using behavioral methods has suggested the importance of infants' self-experience with particular behaviors on their subsequent processing of those behaviors by others (e.g., Kuhl & Meltzoff, 1984; Meltzoff & Brooks, 2008; Sommerville, Woodward & Needham, 2005). Developmental neuroscience data are so far sparse on this issue (van Elk et al., 2008; Saby et al., 2012). One important point is that infants are able to imitate novel actions (Meltzoff, 1988a), showing that generative mappings between perception and production go beyond well-practiced motor routines and habitual actions. Integrating the emerging developmental neuroscience work with the flexibility and generative capacity of infant behavioral imitation is a grand challenge that remains to be met.

Conclusion

In this chapter, we used imitation to elucidate ideas about the development of links between action perception and action production. We reviewed the AIM theory of imitation, which holds that humans have a "supramodal representation" of action that undergirds imitation. Discoveries about

infant imitation suggest that an intrinsic link between seeing an action and producing it exists before language. Although action imitation is present at birth (the youngest infant was 42 minutes old at the time of test), we argued that such imitation may build on prior self-experience with "body babbling."

We reviewed work establishing that imitation is not an uncontrollable impulse. Children select who, when, and what aspects of the adult's display to imitate; moreover, imitative reactions can be regulated by top-down factors, including children's evaluation of the likely adult emotional reactions to the children repeating the actions. Imitation is both cognitive and social: young children recognize having their actions imitated by others. Experiencing such an interpersonal match promotes feelings of affinity and a sense of emotional connection to others viewed as acting "like me" (Meltzoff, 2007a). Mutual imitation is an important aspect of social-cognitive development.

Finally, we considered infant imitation from the viewpoint of developmental cognitive neuroscience. The field is generating new work on the development of neural mirroring mechanisms, and questions arise about how to connect such neuroscience work to the large body of work on behavioral imitation in infancy. We focused here on infant neuroscience work using EEG, with an emphasis on the mu rhythm. Further careful studies are needed for understanding the bidirectional influences of neural and behavioral development. We know that behavior itself provides experience and input that modulates biological plasticity (Gottlieb, 2007; Marshall, 2009), and we know that behavioral evidence often provides the impetus for neuroscience work. Neither field is primary, nor can it stand alone. We need to embrace these bidirectional influences for the emerging field of developmental action science to prosper.

Acknowledgments

We thank K. Moore, P. Kuhl, R. Rao, and T. Shipley. Our research was supported by grants from NSF (SBE-0354453), NIH (HD-22514), and ONR (N000140910097) to ANM; and NIH (HD-68734) and NSF (BCS-0642404) to PJM.

Note

1. Piaget's theory does not deny that young infants could be trained to associate their own movements with similar movements of another. Every time a child poked out his tongue, the parent could do so. The acts might become linked. Piaget (1962)

argued that associationism could not provide a comprehensive theory of imitation, because if it was the mechanism, there would be "haphazard" and "spurious" associations. Mismatched stimulus-response action pairings could be as easily formed as matched ones, and imitation as a learning mechanism would never emerge if one's mother (or caretaker or peers) was not a good imitator.

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V Social Actions

12 Imitation: Associative and Context Dependent

Cecilia Heyes

Introduction

Imitation has been taking a walk on the wild side. Until the mid-1990s, imitation was studied in paradigms where it was either known or believed to be occurring deliberately. Adult human participants were politely instructed to copy observed body movements, and whenever infants or nonhuman primates imitated actions, it was assumed that they had intended to do so. In the last 10 to 15 years, attention has shifted to more wayward forms of imitation. These include unconscious behavioral mimicry, in which people copy the incidental gestures of others, apparently without awareness (Chartrand & Van Baaren, 2009); mirror effects, showing that the passive observation of actions can elicit neural responses associated with the execution of similar actions (Iacoboni, 2009); and automatic imitation, stimulus-response compatibility (SRC) effects in which the observation of task-irrelevant body movements facilitates the performance of similar movements and interferes with the performance of dissimilar movements (Heyes, 2011). This chapter focuses on automatic imitation because it is through studies of this phenomenon that imitation has become for the first time a central focus of action science. Previous research was primarily concerned with the developmental, social, and evolutionary consequences of imitation. It used imitation as an instrument to measure human cognitive and social development, as well as the intelligence of animals. Through the use of automatic imitation paradigms, it has become possible to study the core mechanisms of imitation—the cognitive processes that solve the "correspondence problem" (Brass & Heyes, 2005). These processes allow the perception of an action to be translated into the performance of a topographically similar action, an action in which parts of the observer's body move in the same way, relative to one another, as the parts of the model's body.

Evidence of automatic imitation comes from studies using a special kind of SRC procedure in which the stimulus set includes photographic images of the actions in the response set. For example, in one of the original studies, Stuermer, Aschersleben, and Prinz (2000) asked participants to open and close their hands in response to a color cue (red or blue; the task-relevant stimulus dimension) superimposed on a video of an opening or closing hand (the task-irrelevant stimulus dimension). Correct responses were initiated faster when the irrelevant action stimulus was response compatible (e.g., when an open hand response was made in the presence of an opening hand stimulus) than when the irrelevant action stimulus was response incompatible (e.g., when an open hand response was made in the presence of a closing hand stimulus). In other words, response times (RTs) were shorter in compatible than in incompatible trials. Subsequent studies have reported similar robust effects for a range of finger (Brass, Bekkering, Wohlschlaeger & Prinz, 2000; Brass, Bekkering & Prinz, 2001; Catmur & Heyes, 2011), arm (Gowen, Stanley & Miall, 2008; Kilner, Hamilton & Blakemore, 2007; Kilner, Paulignan & Blakemore, 2003), foot (Bach & Tipper, 2007; Gillmeister, Catmur, Liepelt, Brass & Heyes, 2008), and mouth (Leighton & Heyes, 2010) actions.

Effects of this kind have been called not only "automatic imitation" (Heyes, Bird, Johnson & Haggard, 2005; Liepelt & Brass, 2010; Longo & Bertenthal, 2009; Longo, Kosobud & Bertenthal, 2008; Press, Bird, Walsh & Heyes, 2008) but also "motor priming" (Liepelt, von Cramon & Brass, 2008); "visuomotor priming" (Craighero, Fadiga, Umiltà & Rizzolatti, 1996); "body part priming" (Bach & Tipper, 2007); "effector priming" (Gillmeister et al., 2008); "imitation inhibition" (Brass, Derrfuss & von Cramon, 2005); "imitative compatibility" (Catmur & Heyes, 2011); "movement compatibility" (Brass et al., 2000); "movement interference" (Gowen, Stanley & Miall, 2008); "motor facilitation by action observation" (Edwards, Humphreys & Castiello, 2003); and "motor mimicry" (Spengler, Brass, Kuehn & Schütz-Bosbach, 2010). I prefer the term "automatic imitation" because the word "automatic" captures more vividly than "priming" the apparently involuntary or unintentional nature of the phenomena; and in contrast with "motor" or "visuomotor," "imitation" indicates the topographic specificity of the relationship between visual stimulus and motor response (Heyes, 2011).

Regarding automaticity, several factors suggest that participants in automatic imitation experiments do not intend their behavior to be influenced by the task-irrelevant action stimuli. First, and by definition, participants are not instructed to respond to these stimuli. For example, in the hand

opening/closing paradigm outlined earlier, participants were instructed to respond to the color of the hand stimulus (Stuermer et al., 2000), not to the stimulus dimension that generated the RT difference between compatible and incompatible trials, that is, to the opening or closing properties of the hand stimuli. Second, automatic imitation effects can occur when participants do not intend to direct spatial attention to the action stimuli that generate the effects. For example, hand opening/closing and mouth opening/closing automatic imitation effects have been observed when the imperative cues were presented at fixation, and irrelevant action images appeared in the periphery of the visual field (Leighton & Heyes, 2010). Third, automatic imitation occurs under conditions where it interferes with performance, preventing participants from doing what they have been asked to do—to respond swiftly and accurately to the task-relevant cue. For example, responding is slower in imitatively incompatible trials than in baseline trials where the task-relevant cue is presented in the absence of a task-irrelevant movement stimulus (Bertenthal, Longo & Kosobud, 2006; Brass et al., 2000; Gillmeister et al., 2008). Finally, automatic imitation effects occur when participants are not prepared to perform a response of the incompatible kind. At the beginning of each trial in choice RT paradigms, participants are prepared—they have an active intention—to make each of the responses that could be cued in the trial. However, automatic imitation effects occur not only in choice RT tasks but also in simple RT paradigms where participants are making the same prespecified response in each successive trial (e.g., Heyes et al., 2005).

If we turn to the specificity of the relationship between stimulus and response, ample evidence now indicates that, like intentional imitation, automatic imitation effects depend on topographic features of action—the way in which parts of the body move or are located relative to other parts of the body. For example, the sight of hand opening facilitates the performance of hand opening, not because the stimulus and response actions involve a similar change in relative position (e.g., a movement to the right, or to the left, in external spatial coordinates) but because they both involve movement of the thumb and fingers away from one another and from the palm (Heyes et al., 2005). Thus the hand opening/closing automatic imitation effect is not merely a spatial compatibility effect.

Eleven pairs of action types have been used in experiments on automatic imitation. In seven of these cases, the majority, the evidence clearly shows that automatic imitation effects are not due solely to spatial compatibility: power/precision grip (Chong, Cunnington, Williams & Mattingley, 2009); index finger lifting/tapping (Brass, Bekkering & Prinz, 2001); index/

middle finger movement (Bertenthal et al., 2006); index/little finger abduction (Catmur & Heyes, in press); hand opening/closing (Heyes et al., 2005; Press et al., 2008); mouth opening/closing (Leighton & Heyes, 2010); hand/mouth movement (Leighton & Heyes, 2010). These studies report automatic imitation effects when left–right, up–down, and orthogonal spatial compatibility have been controlled. In 1 of the 11 cases, variables relevant to spatial compatibility have been examined, but the results are not yet conclusive: horizontal/vertical arm movement (Kilner et al., 2003, 2007; Gowen et al., 2008; Stanley et al., 2007). In three cases, the role of spatial compatibility in generating the observed effects has not been investigated systematically: left/right grip orientation (Craighero, Bello, Fadiga & Rizzolatti, 2002; Craighero et al., 1996; Craighero, Fadiga, Rizzolatti & Umiltà, 1998); horizontal/vertical grip orientation (Vogt, Taylor & Hopkins, 2003); and hand/foot movement (Bach, Peatfield & Tipper, 2007; Gillmeister et al., 2008; Wiggett, Hudson, Tipper & Downing, 2011; see Heyes, 2011, for a review).

"Imitation" typically refers to overt behavioral execution of actions that are topographically similar to those observed, but automatic imitation rarely involves overt behavioral execution of topographically matching responses. Automatic imitation effects usually consist of response time, rather than accuracy, differences between compatible and incompatible trials. Therefore automatic imitation appears to be a covert form of imitation—to be related to intentional imitation and overt motor mimicry in much the same way that silent reading is related to reading aloud. In other words, automatic imitation appears to be a phenomenon generated by the same core processes as overt behavioral imitation, but in which the impulse or capacity to copy an action is not fully expressed. If this is correct, automatic imitation paradigms provide an unprecedented opportunity for analytic investigation of the core processes of imitation. In contrast with most intentional imitation paradigms, they permit tight control of stimulus variables, and precise measurement of response characteristics, under conditions where the effects of linguistic and motivational variables are likely to be minimal.

This chapter reviews studies of automatic imitation that bear on an important, long-standing question (Heyes & Bird, 2007): are the core mechanisms of imitation associative or conceptual? Broadly speaking, associative models (fig. 12.1, left side) assume that these mechanisms consist of durable and direct excitatory connections between visual and motor representations of the same topographic features of actions. For example, a visual representation of hand opening is connected to a motor representation of hand opening, so that observation of hand opening directly

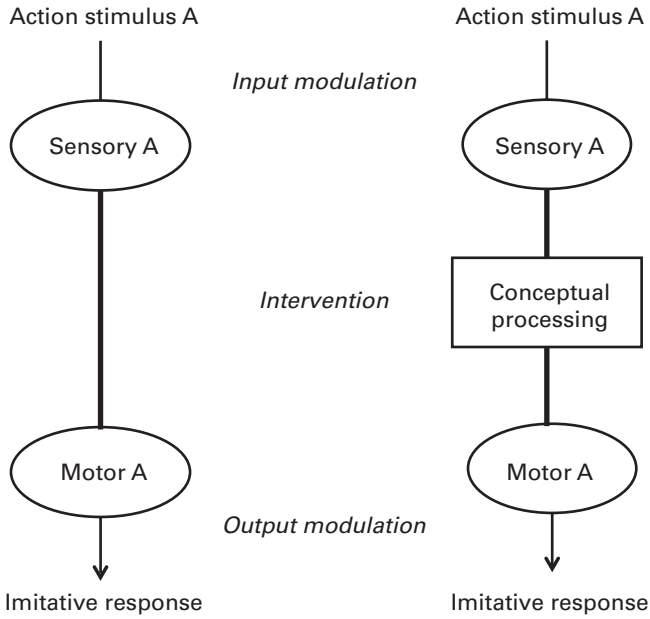

Figure 12.1
Schematic representations of associative (*left*) and conceptual (*right*) models of imitation, showing the loci of input modulation, output modulation, and intervention. In each case, observation of an action, *A*, initially activates a sensory (typically visual) representation of the topographic features of *A*. Associative models suggest that this results directly in the activation of a motor representation of the topographic features of *A*, whereas conceptual models suggest that motor activation occurs only after higher-order processing of some sort. Both types of model allow that context-dependent higher-order processing can modulate imitative performance by influencing the activation of sensory representations (input modulation) and the extent to which motor activation gains control of behavior (output modulation). Conceptual models predict that this kind of processing can also influence the extent to which activation of sensory representations is propagated to corresponding motor representations (intervention).

activates an imitative response. In the associative sequence learning model (Heyes 2001), these connections are described as "matching vertical associations," and in the ideomotor account of imitation (Prinz, 2005) they are known as "common codes." In contrast, conceptual models (fig. 12.1, right side) suggest that when an imitative response occurs, some kind of higher-level processing intervenes in a causal chain between stimulus processing and matching response activation. The nature of this higher-level processing is not specified, but it has been described variously as semantic (Tessari & Rumiati, 2004), symbolic (Bandura, 1986), supramodal (Meltzoff & Moore, 1997), cognitive (Goldenburg, 2006), reconstructive (Csibra, 2008), goal directed (Gattis, Bekkering & Wohlschlaeger, 2002), and conceptual (Jansson, Wilson, Williams & Mon-Williams, 2007).

Both associative and conceptual accounts are consistent with context specificity. They both predict that the occurrence and magnitude of imitative responses will vary with the internal state of the imitator (internal context), and the situation in which the model's behavior is observed (external context), and anticipate that at least some of this variation will be due to the modulation of imitative responses by higher-order cognitive processes. For example, both associative and conceptual accounts are consistent with the modulation of imitative behavior by instruction-specific or situation-specific beliefs about the action stimuli. However, associative models imply that broadly intentional processes can modulate imitative performance only by influencing the processing of the action stimulus (input modulation) or by influencing the extent to which activation of a motor representation is either inhibited or allowed to influence overt responding (output modulation). In contrast, conceptual models suggest that higher-order processes can also "intervene," that is, modulate imitation by changing the extent to which activation of the stimulus representation results in activation of the response representation. Associative models are not consistent with intervention because they suggest that imitation depends on direct links in long-term memory between sensory and motor representations of the same action, and it is the nature of such links that their strength cannot be changed by higher-order processes. In contrast, conceptual models predict intervention because they suggest that imitation depends on a cognitive architecture in which some kind of higher-order cognitive process always occurs after activation of a sensory representation of the action stimulus and before activation of a motor representation of the same action. This kind of intermediate cognitive process would provide a natural locus for contextual factors to influence imitative performance.

The first section of this chapter reviews evidence that automatic imitation is subject to input modulation. This evidence currently consists of studies showing that contextual variables can influence the magnitude of automatic imitation effects by modulating attentional variables. The second section examines studies that have been interpreted as demonstrating output modulation. These suggest that social cognitive variables can influence automatic imitation, not by changing the properties of a long-term sensorimotor link but by inhibiting motor activation after that link has operated. The third section discusses studies of conceptual compatibility and counterimitative task set, which have been interpreted as evidence of intervention: evidence that contextual variables can modulate automatic imitation by altering the process that translates activation of a stimulus representation into activation of a response representation. The final part of the chapter suggests potentially productive directions for future work on the mechanisms of imitation, including examination of the role of conditional learning in generating context effects.

Input Modulation

Automatic imitation has been reported when task-irrelevant movement stimuli were presented in the periphery of the visual field (Leighton & Heyes, 2010). This suggests that automatic imitation can occur when participants are not directing their attention to the stimuli that are generating the effect. However, evidence also suggests that top-down variations in spatial attention and feature selection can influence the magnitude of automatic imitation effects.

Several studies of animacy—comparing the magnitude of automatic imitation effects generated by natural human movements and by artificial, impossible, or robotic movements—have pointed to this conclusion (Liepelt & Brass, 2010; Longo & Bertenthal, 2009; Longo et al., 2008). For example, Longo et al. (2008) asked participants to respond to the left–right spatial position of index and middle finger tapping movements that were either possible (normal joint movements) or impossible (abnormal joint movements). When the task instructions made no reference to the possibility variable, the automatic imitation effect (e.g., faster index finger responses to index than to middle finger stimuli) was of equal magnitude in the possible and impossible conditions. However, in another experiment, where participants were told that they would see both natural and impossible movements, an automatic imitation effect occurred only in the blocks where possible actions were presented.

These results were interpreted as effects of instructions on attention (Longo & Bertenthal, 2009; Longo et al., 2008). When the instructions did not mention the impossible or computer-generated character of the stimuli, participants attended to the end point of each movement, and both possible/photographic and impossible/computer-generated movements produced an automatic imitation effect. When the instructions alluded to the possibility variable, participants shifted their attention from movement end points to movement kinematics, and the impossible/computer-generated stimuli failed to produce a substantial automatic imitation effect because their kinematics were unfamiliar or dissimilar to those of the tapping responses.

Other animacy studies have examined the magnitude of automatic imitation effects produced by natural human movement stimuli as a function of participants' beliefs about the origins of those stimuli. For example, before testing participants with index and middle finger movements of a gloved human hand, Liepelt and Brass (2010) told one group of participants, with an illustration, that the movements had been generated by a wooden hand. This group showed a smaller automatic imitation effect than the group that believed they were observing human movements. As the authors acknowledged (Liepelt & Brass, 2010), like the animacy effects reported by Longo and colleagues (Longo, Kosobud & Bertenthal, 2008; Longo & Bertenthal, 2009), this result could have been due to closer attention to movement kinematics in the wooden hand group. If the index/middle finger automatic imitation effect depends on effector priming, rather than movement priming, focusing attention on movement kinematics would be expected to erode the magnitude of the effect.

In experiments similar to those of Longo et al. (2008; Longo & Bertenthal, 2009) and Liepelt et al. (2008; Liepelt & Brass, 2010), Press, Gillmeister, and Heyes (2006) found that hand open/close automatic imitation effects were not modulated by instructions concerning the human or robotic origins of the movement stimuli or by whether the stimulus movements were performed by a hand with a natural human wrist or a robotic wire wrist. These negative results are unlikely to have been due to test insensitivity because the same paradigm has shown that automatic imitation can be modulated by intrinsic properties of the movement stimuli (Press, Bird, Flach & Heyes, 2005; Press et al., 2006). Therefore they imply that for reasons that are yet to be established, automatic imitation of hand opening/closing, assessed in a simple RT task, is less susceptible to the influence of attention than automatic imitation of index/little finger movements, assessed in a choice RT task.

More direct evidence that automatic imitation can be modulated by attention comes from a study that varied the location of the imperative cue relative to the action stimuli eliciting the effect (Bach et al., 2007, experiment 1). Participants were instructed to respond with their foot or their hand, depending on the color of a dot presented near the head, hand, or foot in whole-body images depicting hand or foot action. An automatic imitation effect (e.g., faster foot responses when the actor was performing a foot than a hand action) occurred when the imperative stimuli appeared close to the acting effector, but not when the dots appeared close to the actor's head.

In another study designed explicitly to examine the effect of attention on automatic imitation, Chong et al. (2009, experiment 2) presented a red or blue diamond superimposed on a hand in a power or precision grip posture. An automatic imitation effect (e.g., faster execution of power grip with a power than a precision grip cue) occurred when participants were instructed to use stimulus grip as the go/no go signal (i.e., to decide whether or not a prespecified response should be made in that trial), but not when they were instructed to use color as the go/no go signal.

This brief review shows that both direct (Bach et al., 2007) and indirect (Liepelt & Brass, 2010; Longo & Bertenthal, 2009; Longo et al., 2008) evidence indicates that the magnitude of automatic imitation effects can be modulated by attention. This evidence of input modulation is consistent with both associative and conceptual models of imitation.

Output Modulation

Research relevant to output modulation has been dominated by studies showing, through a variety of methods, that the magnitude of automatic imitation effects can be influenced by social cognitive processes. For example, Spengler, Brass et al. (2010) found that the index/middle finger automatic imitation effect was attenuated when self-focus was encouraged by allowing participants to view their own body in a mirror during testing or by requiring them to make evaluative self-referential judgments between trials. Similarly, Leighton, Bird, Orsini, and Heyes (2010) tested participants in the hand open/close paradigm immediately after they had completed a scrambled-sentence task. The automatic imitation effect was attenuated if the sentence task included antisocial words (e.g., rebel, independent, disagreeable, alone) and enhanced if it included prosocial words (e.g., affiliate, friend, cooperate, together), relative to a condition in which the sentence task included only neutral words. Also using the hand open/close procedure,

Wang, Newport, and Hamilton (2011) found a larger automatic imitation effect when the movement stimulus was preceded by the actor making direct eye contact with the participant than when it was preceded by averted gaze or by a centrally located flash of light.

These findings from behavioral studies involving neurologically intact participants support those of previous research involving functional imaging and patients with brain lesions. The imaging studies have shown consistently that two cortical areas associated with social cognitive functions, the anterior fronto-median cortex (aFMC) and the temporo-parietal junction (TPJ), are more active during incompatible than during compatible trials in the index lift/tap (Brass, Zysset & von Cramon, 2001) and index/middle finger (Brass et al., 2005; Spengler, von Cramon & Brass, 2010) automatic imitation paradigms. The neuropsychological studies have indicated that, in patients with frontal lesions and in controls, the magnitude of the index/middle finger automatic imitation effect is correlated with performance on an advanced theory-of-mind task, and in patients with TPJ lesions, it is correlated with indices of empathy, visual perspective taking, and theory of mind (Spengler, Von Cramon & Brass, 2010). In all cases, a larger automatic imitation effect predicted weaker performance on measures of social cognitive functioning.

Studies involving participants with autism spectrum condition (ASC), who are known to have impairments in social cognitive functioning, also suggest that social cognitive processes can modulate automatic imitation. Compared with controls, adults with ASC show an enhanced automatic imitation effect in the hand open/close procedure (Bird, Leighton, Press & Heyes, 2007). Furthermore, in the index/middle finger procedure, the magnitude of their automatic imitation effects is not influenced by prosocial and antisocial priming using a scrambled-sentence task (Cook & Bird, 2012). Similarly, Bach and Tipper (2007) found a correlation between Autism Spectrum Quotient scores and the extent to which completion of a hand/foot automatic imitation procedure influenced participants' judgments about the personality characteristics of the actors observed during the procedure. For example, participants with high scores were more inclined to judge as "sporty" an actor who had been observed kicking a ball, rather than typing on a keyboard, when the participant was making foot responses.

These findings have been interpreted as examples of output modulation, suggesting that social cognitive processes modulate the magnitude of automatic imitation effects by influencing the extent to which corresponding motor activation is either inhibited or allowed to influence overt

behavioral performance (Bien, Roebroeck, Goebel & Sack, 2009; Brass, Ruby & Spengler, 2009). More specifically, Brass et al. (2009) have proposed that two social cognitive functions are involved in the modulation of automatic imitation. The first function, associated with the TPJ, makes "agency" judgments; it classifies an observed body movement as either self-generated or other generated. The second function, associated with the aFMC, "is required to enforce one's own motor intention against the externally triggered response tendency." In other words, the aFMC mediates higher-order intentional processes that oppose the behavioral expression of motor activation generated by a direct sensorimotor association. Factors influencing the efficiency of either or both functions—durably, as in the cases of brain injury and ASC, or transiently, via self-focus and social priming procedures—could have an impact on the magnitude of automatic imitation effects. For example, weak enforcement of the participant's own intentions (based on task instructions) could be a direct effect of brain injury or social priming, or secondary to a reduction in the efficiency with which body movement stimuli are classified as other generated rather than self-generated. In either case, weak enforcement of a participant's own intentions would be expected to result in faster responding in imitatively compatible trials and slower responding in imitatively incompatible trials, because it would leave associatively activated motor representations relatively unopposed in gaining control of behavior.

We still have much to learn about the interaction between automatic imitation and other social cognitive functions. However, at present, research in this area suggests that higher social cognitive functions modulate automatic imitation, not by changing the process that normally generates corresponding motor activation but by regulating the behavioral output from this process. Thus, consistent with both associative and conceptual models of imitation, higher social cognitive processes appear to contribute to output modulation rather than intervention.

Intervention

Studies of conceptual compatibility and counterimitative task set have been interpreted as evidence of intervention: context-related intentional processes can modulate automatic imitation, not only at input and output but also by changing the process that translates activation of a stimulus representation into activation of a response representation. If this is correct, it is unlikely that the translation process is mediated by long-term sensorimotor associations.

Jansson et al. (2007) have suggested that automatic imitation effects may be due to "conceptual compatibility." For example, the sight of hand opening may activate a verbal or semantic representation of "opening," rather than a motor representation of hand opening, that is, a specific, topographically similar response. In this case, the process producing "automatic" imitation effects would be mediated by higher-order representations, and therefore it would be likely that higher-order processes could intervene to prevent it from running its course.

In support of their proposal, Jansson et al. (2007, experiment 2) showed that a compatibility effect could be obtained with hand opening/closing responses not only when the stimuli depicted opening and closing hand actions but also when they consisted of two dots moving apart (opening) or together (closing). However, this result is ambiguous. It could be that the hand and dot compatibility effects were mediated by the same conceptual process, but it is at least equally plausible that the dot effect was mediated by a conceptual process (or by orthogonal spatial compatibility; see Press et al., 2008), whereas the hand effect was due to direct activation of motor responses by action stimuli.

An experiment by Leighton and Heyes (2010) provided a stronger test of the conceptual compatibility hypothesis proposed by Jansson et al. (2007). If the sight of hand opening activates an abstract verbal or semantic representation of "opening," rather than a specific motor representation of hand opening, one would expect hand opening stimuli to be equally effective in priming hand opening and mouth opening responses. However, the results reported by Leighton and Heyes (2010, experiment 3) were contrary to this prediction. They used a procedure in which color stimuli cued one of four responses in each trial—hand open, hand close, mouth open, mouth close—and this imperative cue was accompanied by an irrelevant stimulus depicting one of the same four actions. They found that the open/close compatibility effect was significantly greater when the stimulus effector was response compatible than when it was response incompatible. For example, open mouth responses were faster in the presence of open hand than of close hand stimuli, but the effect of the irrelevant hand stimuli was greater when participants were making open hand, than open mouth, responses. This pattern of results suggests that, rather than being conceptually mediated, the hand open/close compatibility effect is due to direct, associative activation by movement observation of motor representations coding topographically similar responses.

In another study that has been interpreted as providing evidence of intervention, Van Schie, Van Waterschoot, and Bekkering (2008) showed

that an automatic imitation effect can be reversed when trials in which the action cue is task irrelevant are embedded in a counterimitation task (for similar effects, see Heyes & Ray, 2004; Ocampo & Kritikos, 2009). In each trial in these experiments, participants saw an actor grasping either the base of an object with a power grip or the upper part of the object using a precision grip. In imitation blocks, participants were asked to do the same as the actor (e.g., to respond to a power grip using a power grip), and in counterimitation blocks they were instructed to perform the opposite action (e.g., to respond to a power grip using a precision grip). The findings of interest were from probe trials presented in each of these block types. In probe trials, a component of the stimulus video (hand, object, or table) was colored green, indicating that the participant should make a prespecified response—for example, use a power grip, regardless of the grip type applied by the model. In imitation blocks, probe trial responding was faster when the action stimulus was compatible with the prespecified response, but in counterimitation blocks, probe trial responding was slower when the action stimulus was compatible with the prespecified response.

This striking reversal effect has been taken to indicate that higher-order processes can intervene to determine whether perceptual analysis of action stimuli results in the activation of topographically similar or topographically dissimilar motor representations. This interpretation has two problems. First, in this experiment, grip type (power versus precision) was confounded with the part of the object grasped (large base versus small top), and therefore there is a risk that responses were primed not by topographic features of body movement but by spatial properties of the object part (Heyes, 2011). Second, the reversal effect is formally identical to the Hedge and Marsh effect (Hedge & Marsh, 1975) and can be explained in terms of "logical recoding," which is a form of output modulation (De Jong, Liang & Lauber, 1994).

The output modulation account of the reversal effect reported by Van Schie et al. (2008) assumes that standard (nonreversed) spatial compatibility and automatic imitation effects can be explained by "dual route" processing in the following way. Once it has been identified through perceptual analysis, the task-relevant stimulus activates the correct response via an intentional route. This route is often modeled as a short-term stimulus-response (S-R) connection: an excitatory link between a stimulus representation and a response representation, which is established on the basis of task instructions and held in short-term memory for the duration of the task (Barber & O'Leary, 1997; Zorzi & Umiltà, 1995). In addition, the task-irrelevant stimulus activates a similar or "corresponding" response via an

automatic route. This route is typically modeled as a long-term S-R connection: an excitatory link between a stimulus representation and a response representation, which is held in long-term memory. If the intentional and automatic routes activate the same response representation (compatible trials), the correct response is executed rapidly. However, if the two routes activate different response representations (incompatible trials), the incorrect response, activated via the automatic route, must be inhibited in favor of the correct response. This takes extra time, and therefore responding is slower in incompatible trials.

The output modulation account of the reversal effect reported by Van Schie et al. (2008) assumes that incongruent mapping instructions are logically recoded, or overgeneralized, from the task trials, in which location and grip are response relevant, to the probe trials, in which color is response relevant. Consequently, if we take counterimitation blocks as an example, the intentional route includes response rules, or short-term S-R links, connecting incompatible stimuli and responses. These compete with the long-term sensorimotor associations that connect compatible stimuli and responses and constitute the automatic route. Unless responses are made very fast, when automatic activation is strong, performance is dominated by the short-term intentional links that promote incompatible responding, and a reversal of the usual compatibility effect is observed (De Jong et al., 1994). If this account is correct, the reversed automatic imitation effect reported by Van Schie and colleagues does not show that contextual variables can modulate imitative performance by acting on a conceptual process that reliably occurs between stimulus processing and activation of a corresponding motor representation. In other words, their reversal effect is not an example of intervention.

Thus research on conceptual compatibility and the influence of a counterimitative task set does not currently provide compelling evidence that higher-order cognition can intervene in the process mediating automatic imitation. The conceptual compatibility hypothesis is inconsistent with the effector dependence of automatic imitation, and the effect of counterimitative task set could be due to logical recoding, that is, output modulation by intentional processes.

Conditional Learning

This chapter has distinguished three ways in which aspects of the social and nonsocial context could, in principle, have an impact on automatic imitation via higher-order processing: input modulation, where broadly

attentional processes influence the extent of action stimulus processing; output modulation, where imitative motor representations are inhibited or allowed to gain control of overt behavior; and intervention, where context-dependent intentions have a direct effect on the process that converts activation of an action stimulus representation into activation of a topographically similar response representation. As predicted by associative models of imitation, the review found evidence of input modulation and output modulation, but not of intervention. This tripartite scheme could be useful in future studies of imitation and related phenomena such as unconscious behavioral mimicry and mirror effects (Heyes, 2011).

However, to make further progress in understanding the core mechanisms of imitation—those that translate sensory representations of action into topographically similar motor representations—we need empirical studies designed explicitly to distinguish input and output modulation from intervention. To design such studies, it will almost certainly be necessary to develop conceptual models that specify the kind of higher-order processing that may constitute a core mechanism of imitation. Without this specification—without a clear picture of the kind of process in which intervention is supposed to intervene—it will remain extremely difficult for conceptual models to make testable predictions.

Associative models of imitation also require further elaboration, both to exploit more fully the wealth of information about associative learning accumulated through research on conditioning and to accommodate the full range of context effects likely to emerge in the next decade (Massen & Prinz, 2009). As a first step, the remainder of this section suggests that it would be fruitful for associative models of imitation to incorporate what is known about conditional learning (e.g., Bonardi, 1998).

It will be helpful for associative models of imitation to borrow theoretical and empirical resources from associative learning theory only if the long-term sensorimotor links that mediate imitation are predominantly learned, and learned via the same processes that produce Pavlovian and instrumental conditioning phenomena. A substantial body of evidence now suggests that the long-term sensorimotor links are learned (see Heyes, 2011, for a review). For example, this evidence shows that automatic imitation and mirror effects can be enhanced (Press, Gillmeister & Heyes, 2007), abolished (Heyes et al., 2005; Gillmeister et al., 2008; Wiggett et al., 2011), and even reversed (Catmur et al., 2008; Catmur, Mars, Rushworth & Heyes, 2011; Catmur, Walsh & Heyes, 2007) by novel sensorimotor experience. Some of the clearest evidence that this learning depends on the same processes as conditioning comes from a study showing that, like the acquisition of

conditioned responses (Dickinson & Charnock, 1985; Elsner & Hommel, 2004), it is sensitive to the contingency or predictive relationship between events (Cook, Press, Dickinson & Heyes, 2010).

Cook et al. (2010) followed up an experiment in which participants were tested for automatic imitation of hand opening/closing in a simple RT task 24 hours after they had performed 432 trials of a choice RT task in which closing hand responses were made to opening hand stimuli and opening hand responses were made to closing hand stimuli (incompatible group), or vice versa (control group). In this experiment, a significant automatic imitation effect (e.g., faster hand opening responses in the presence of hand opening than of hand closing stimuli) was observed in the control group, but not in the incompatible group (Heyes et al., 2005). Using the same procedure, Cook et al. (2010) found that incompatible sensorimotor experience abolished automatic imitation only when there was a positive contingency between hand movement stimuli and hand movement responses during training. When this contingency was eroded, for example, by including additional training trials in which responses occurred in the absence of movement stimuli, the effect of training was significantly reduced.

Research on conditional learning within the associative tradition has shown that contextual variables—known as "discriminative stimuli" or "occasion setters"—can modulate the learned behavior of animals such as rats and pigeons. For example, Colwill and Rescorla (1990, experiment 2) trained rats in an environment where they could make two responses, lever pressing (R1) and chain pulling (R2), for two kinds of outcomes, sucrose solution (O1) and dry food pellets (O2), in the presence of two contextual stimuli, a noise (S1) and a light (S2). When a noise sounded (S1), lever pressing produced sucrose (R1 > O1), and chain pulling produced pellets (R2 > O2); but when the light was presented, lever pressing produced pellets (R1 > O2), and chain pulling produced sucrose (R2 > O1). (The design was fully counterbalanced.) One of the two outcomes was then devalued by pairing with lithium chloride. In a subsequent test, where no outcomes were available, the rats' behavior was precisely modulated by the contextual stimuli: guided by these stimuli, they preferred to make the response that would have yielded the nondevalued outcome. For example, rats that had been averted to sucrose pulled the chain more than they pressed the lever in the presence of the noise, and pressed the lever more than they pulled the chain in the presence of the light.

Experiments of this kind demonstrate that complex contextual modulation of behavior can occur in relatively "simple" animals. They have also

provided information about the way in which associative mechanisms can produce contextual modulation. Two models—hierarchical and configural—have substantial empirical support. In the hierarchical model (Holland, 1983; Bonardi 1998), binary associations between a response and an outcome (e.g., R1 > O1) function as a unit that itself becomes associated with a contextual cue (e.g., S1). In other words, the contextual cue acts as an "and-gate" allowing activation of the response representation to be propagated to the outcome representation, or vice versa. In the configural model (Brandon & Wagner, 1998; Wilson & Pearce, 1992), the learner encodes the response-in-context (e.g., R1-in-C1), and this configural representation becomes associated with an outcome (e.g., O1). For example, lever-pressing-in-noise becomes associated with sucrose, whereas lever-pressing-in-light becomes associated with pellets.

Thus studies of conditioning in animals suggest that if it is based on learned sensorimotor associations, the contextual specificity of imitative performance could be due not only to input modulation and output modulation but also to conditional learning. As this chapter indicates, all the context effects reported to date in the literature on automatic imitation can be explained in terms of input and output modulation; they do not yet call for an explanation in terms of conditional learning. However, it is likely that training effects on automatic imitation depend, at least in part, on conditional learning. Consider the case, described earlier, where a relatively brief period of incompatible sensorimotor training (hand opening responses to hand closing stimuli, and vice versa) abolished the hand opening/closing automatic imitation effect (Heyes et al., 2005; Cook et al., 2010). It is possible that this training left intact the sensorimotor links that previously generated automatic imitation—links between topographically corresponding sensory and motor representations (open-open, close-close)—and established a new pair of noncorresponding associations (open-close, close-open) that were under the control of the training context. To test this hypothesis, it would be necessary to conduct incompatible sensorimotor training in a distinctive context and to compare its effects on automatic imitation in the training context and in an alternative context. If the effects of training are mediated by conditional learning, one would expect them to be stronger in the training context (Cook, Dickinson & Heyes, 2012).

More speculatively, conditional learning may also play a part in producing context effects on behavioral mimicry. For example, the physical characteristics of in-group members (e.g., accents, clothing) may act as occasion setters for the sensorimotor links underlying the enhanced mimicry of

in-group members in naturalistic social settings (Yabar, Johnston, Miles & Peace, 2006). Similarly, in the case of tool use actions, pivot points may act as occasion setters for sensorimotor associations relating simple spatial properties of action (e.g., toward versus away) to lever movements (e.g., up versus down) (Massen & Prinz, 2009).

Conclusion

Automatic imitation is a type of stimulus-response compatibility effect in which the topographical features of task-irrelevant action stimuli facilitate similar, and interfere with dissimilar, responses. This chapter has reviewed research on automatic imitation indicating that it is subject to input modulation by attentional processes, and output modulation by inhibitory processes, but not to intervention; higher-order cognition does not act directly on the processes that convert visual into motor representations of action. The lack of evidence of intervention suggests that even when automatic imitation effects are context dependent, they are mediated by associative rather than conceptual processes—by learned, long-term associations between sensory and motor representations of the same actions. This conclusion is consistent with the associative sequence learning (ASL) (Heyes, 2001) and ideomotor accounts of imitation (Prinz, 2005).

Automatic imitation is one of several "wayward" or unintentional forms of imitation that have been investigated intensively in the last 10 to 15 years. Others include unconscious behavioral mimicry and mirror effects. Drawing on evidence that lies beyond the scope of this chapter (e.g., Leighton, Bird & Heyes, 2010), both the ASL model and ideomotor theory suggest that these wayward forms of imitation are mediated by the same core processes as intentional imitation. If so, the research reviewed here suggests that both when we are trying to imitate and when imitative responses are elicited by body movement stimuli, the infamous correspondence problem (Brass & Heyes, 2005) is solved by associative processes. Higher-order cognitive processes can influence imitative performance, but the core competence—the ability to convert the sight of a body movement into matching motor output—depends on learned, long-term sensorimotor associations.

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13 Joint Action: From Perception-Action Links to Shared Representations

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Introduction

Imagine a pianist and a violinist performing a duet together. Each performer must plan and produce a long sequence of precisely timed actions, and each must monitor the perceptual consequences of those actions to ensure that the correct sequence of sounds is produced. Successful performance requires that the pianist and violinist perform these tasks jointly rather than individually: each performer must time his or her actions to coincide with the other's, each must modify his or her action plans depending on the perception and prediction of the other's actions, and each must monitor not only the perceptual consequences of his or her own actions but also the combined outcome of the two performers' actions. Thus the two performers' actions and perceptions are intimately linked (see Kiefer & Barsalou, this volume); one performer's actions and perceptions can hardly be understood without the other's.

It is not only in ensemble music performance that one person's actions and perceptions are linked with another's. Joint actions, in which two or more people coordinate their actions in space and time to bring about a change in the environment (Sebanz, Bekkering & Knoblich, 2006), abound in daily life. Examples range from exchanging money with a cashier or cooking dinner with a friend to dancing, playing sports, and having conversations (Clark, 1996). In this chapter, we aim to elucidate the basic mechanisms of perception and action that underlie such joint actions, using music performance as a particularly rich example. We focus on two types of mechanisms. We begin with close links between perception and action, which support joint action by evoking similar actions or similar timing of actions in multiple individuals (Marsh, Richardson & Schmidt, 2009). We then turn to shared representations of coperformers' tasks and perceptions. These representations support joint action by specifying how

each individual's actions are planned, monitored, and controlled (Vesper, Butterfill, Knoblich & Sebanz, 2010).

Close Links between Perception and Action

Close links between perception and action lead to interpersonal coordination because two or more individuals process similar perceptual or motor information, which induces them to act in similar ways. We distinguish two related phenomena evoked by perception-action links: entrainment and perception-action matching. Entrainment leads people to align their actions in time (Schmidt & Richardson, 2008), even when their actions differ. For example, when a pianist and violinist perform a duet, they produce different actions that are nevertheless nearly simultaneous. In contrast, perception-action matching induces people to perform similar actions (Brass & Heyes, 2005) or actions with similar perceptual consequences (Hommel, Müsseler, Aschersleben & Prinz, 2001; Prinz, 1997) without necessarily being aligned in time. For example, people engaged in conversation tend to mimic each other's actions at variable temporal delays (Chartrand & Bargh, 1999). Both entrainment and perception-action matching can result in coordinated behavior regardless of whether or not the individuals involved plan to perform a joint action, as when audience members clap in unison during spontaneous applause (Néda, Ravasz, Brechet, Vicsek & Barabási, 2000), or when people yawn upon seeing someone else do so (Provine, 1986). Coordination that results from these processes is therefore referred to as emergent coordination (Knoblich, Butterfill & Sebanz, 2011), though these processes also support action alignment in planned coordination, as we will describe next.

Entrainment: Alignment in Time

One striking aspect of duet music performance is the close temporal alignment between performers. Ensemble musicians typically produce nominally simultaneous tones with asynchronies of around 30 to 50 ms (Rasch, 1979), and asynchronies are even smaller for simple pieces performed on the same instrument (Loehr & Palmer, 2011). Entrainment is one mechanism by which this precise temporal alignment may be achieved. Proponents of entrainment as an explanation for interpersonal coordination argue that the same mathematical principles that underlie coordination between physical systems (specifically, the nonlinear dynamics of coupled oscillation) also underlie coordination between people (see Pikovsky, Rosenblum & Kurths, 2001, for an accessible introduction to the mathe-

matics of coupled oscillation). By this account, cognitive representations of perceptions and actions are not necessary. Just as two pendulums suspended from the same beam will come to swing at the same rate because they can influence each other directly through the mechanical connection between them, so will two people's actions become aligned in time when they can influence each other directly through shared visual, auditory, or haptic information (Kelso, 2001; Schmidt, Carello & Turvey, 1990; for a review, see Schmidt & Richardson, 2008).

Evidence of Entrainment in Joint Action

The mathematical principles underlying coupled oscillations predict patterns of interpersonal coordination that arise when partners coordinate rhythmic movements based on visual perception of each other's movements. For example, people show two stable modes of coordination when they are asked to swing pendulums back and forth together: in-phase coordination, in which both pendulums are in the same position in the movement cycle (e.g., both swung forward) at the same time, and antiphase coordination, in which the pendulums are in opposite positions at the same time (when one pendulum is swung forward, the other is swung backward; Schmidt et al., 1990). Antiphase coordination is less stable than in-phase coordination, and because of this reduced stability, a sudden transition to in-phase coordination occurs as the rate at which participants swing their pendulums increases (Schmidt, Bienvenu, Fitzpatrick & Amazeen, 1998). Each of these patterns is predicted based on the Haken-Kelso-Bunz model of coupled oscillations (Haken, Kelso & Bunz, 1985); thus when two people coordinate their rhythmic movements based on visual perception, the temporal alignment they produce reflects the dynamics of coupled oscillations.

The dynamics of coupled oscillation are also evident in coordination based on auditory perception. When people listen to music alone, their internal rhythms (e.g., sense of the musical beat, as sometimes manifest in tapping along with music) become entrained to the music (Large, 2008; Large & Palmer, 2002). The mathematical principles underlying coupled oscillation can explain, for example, how people track rate changes in expressive music performance, in which performers slow down or speed up to convey a particular musical interpretation (Large & Palmer, 2002). Recent work has shown that these same principles can explain how people adapt to rate changes that may arise when they play music together: musicians are better able to coordinate their performances with auditory sequences that slow down than sequences that speed up, as predicted based

on oscillator dynamics (Loehr, Large & Palmer, 2011). Thus the dynamics of coupled oscillation may underlie people's ability to maintain precise temporal coordination despite fluctuations in their coperformers' timing.

Entrainment based on auditory perception is also evident when people engage in conversation. Several studies have shown that the body movements of two people having a conversation become aligned in time even when they are not able to see each other. For example, two people's postural sway (automatic movements that keep the body in a stable posture) is more similar when they discuss cartoon pictures with each other than when each discusses them with a different partner. This is true whether the participants can see each other or not (Shockley, Santana & Fowler, 2003). Shared postural sway is greater when conversation partners speak more quickly and produce words with similar stress patterns, suggesting that the coordination of articulatory actions may drive the entrainment (Shockley, Baker, Richardson & Fowler, 2007). Entrainment may also explain why people's eye movements become temporally aligned when they converse with each other (Richardson, Dale & Kirkham, 2007).

Top-Down Influences on Entrainment

Entrainment can be modulated top-down by, for example, people's intentions to coordinate. When pairs of participants swing pendulums in sight of each other, but under instructions to maintain their own preferred rate, they show similar patterns of coordination as when they intend to coordinate with each other. However, this unintentional coordination is weaker than intentional coordination (Schmidt & O'Brien, 1997). Similarly, the intention to coordinate enhances entrainment in young children. They are more accurate at synchronizing their actions with a drumbeat, and can synchronize with a wider range of intervals, when they drum along with an experimenter than when they drum with a mechanical device (Kirschner & Tomasello, 2009). Together, these findings indicate that the intention to coordinate enhances entrainment, and suggest that entraining with a more adept partner may allow novices to discover new ways of performing.

Indirect Benefits of Entrainment

Entrainment may benefit joint action indirectly by moderating the relationship between coactors, as well as coactors' cognitive processing. People who have moved in synchrony with each other report stronger feelings of liking, connectedness, and trust toward each other and are more likely to cooperate with each other in economic games than people who have moved asynchronously (Hove & Risen, 2009; Wiltermuth & Heath, 2009).

Participants who move in synchrony with an experimenter remember more words spoken by the experimenter and better recognize the experimenter's face in surprise memory tests following the interaction (Macrae, Duffy, Miles & Lawrence, 2008), suggesting that entraining with a partner may increase the attention allocated to that partner. Participants who move in synchrony with a partner also show increased perceptual sensitivity to object motion, as well as increased responsiveness to the partner's motion during a subsequent joint action, compared to pairs who have not moved in synchrony (Valdesolo, Ouyang & DeSteno, 2010). Thus joint performance may benefit from improvements in individual memory and perceptual processing that result from having been entrained with a partner.

In sum, entrainment can explain how people's actions become tightly coordinated in time during joint action. When people intend to synchronize their actions with each other, they display coordination patterns that follow the mathematical principles governing coupled oscillators. Entrainment also occurs when people engage in joint actions without the explicit goal to synchronize their movements, as evident in the coupling of body and eye movements between conversation partners and in the weaker temporal coordination that arises when people can simply see each other's movements. Entrainment may also benefit joint action indirectly by increasing feelings of interpersonal affiliation and improving cognitive processing during and after the synchronized action.

Perception-Action Matching: Similarity in Goals and Movements

Whereas entrainment can explain why people align their actions in time, perception-action matching can explain why people produce similar actions or actions with similar perceptual consequences. Perception-action matching relies on the common representations that have been proposed to underlie perception and action (Hommel et al., 2001; Jeannerod, 1999; Prinz, 1997). These common representations allow people to match the actions they perceive onto their own action repertoires. This match can be based on movement similarity, as when observing someone dance activates a representation of dancing movements, or on similarity of actor-object relations, as when observing someone grasp an apple activates a representation of grasping round objects (Knoblich et al., 2011). Matching a perceived action or actor-object relation onto one's own action repertoire can induce in the perceiver a tendency to produce an action similar to the perceived action (Brass, Bekkering & Prinz, 2001; Stürmer, Aschersleben & Prinz, 2000) and can allow the perceiver to make predictions about how the perceived action will unfold (Sebanz & Knoblich, 2009; Wilson &

Knoblich, 2005). Both of these processes can lead to coordination even in the absence of an intention to coordinate (i.e., emergent coordination; Knoblich et al., 2011), and both also support planned joint action.

Perception-Action Matching during Observation

Much of the evidence for perception-action matching comes from studies that involve one individual observing another individual's action. Neurophysiological studies have established that in monkeys, groups of neurons discharge both when an action is observed and when it is executed (Rizzolatti, Fadiga, Gallese & Fogassi, 1996), and in humans, similar brain regions are activated when an action is perceived and when it is executed (Rizzolatti & Craighero, 2004; Rizzolatti & Sinigaglia, 2010). The behavioral literature has in turn established that observing someone produce an action facilitates production of a similar action by the observer. For example, people are faster to perform a grasping action when they concurrently watch a video of a hand performing a grasping action compared to a spreading action (Stürmer et al., 2000). Similar facilitation effects occur with goal-directed actions; observing someone kick a ball facilitates foot responses, and observing someone type on a keyboard facilitates finger responses (Bach & Tipper, 2007). Furthermore, perceived actions interfere with produced actions when the two do not correspond: people's vertical arm movements are more variable when they concurrently observe horizontal arm movements compared to when they observe vertical arm movements (Kilner, Paulignan & Blakemore, 2003). Together, these findings indicate that observing an action leads to automatic activation of that action in the observer.

The effects of perceiving an action on production of that action can be modulated by the intentions of the perceiver or the actor. This is important for joint action because it often requires complementary rather than corresponding actions. In an investigation of how an observer's intentions modulate action facilitation, van Schie, van Waterschoot, and Bekkering (2008) instructed participants either to imitate an observed coactor's grip or to produce a complementary grip (as if taking the object from the coactor). In some trials, participants responded to a color cue by producing one of the two grips, regardless of the interaction context. Participants were faster to produce the observed grip in the imitation context but were faster to produce the complementary grip in the complementary action context. Thus the observer's intention to produce a complementary action overrode the automatic activation of imitative actions. Likewise, the actor's intentions modulate the movements induced by action observation. For example,

observing a person balancing on a foam roller does not induce imitative movements (body tilt in the same direction as the actor's) but induces compensatory movements (body tilt in the opposite direction to the actor's, as would be necessary for the actor to maintain balance; Sebanz & Shiffrar, 2007). Together, these studies on action observation suggest that perception-action matching may facilitate joint action by inducing similar or complementary action tendencies in people who perceive each other's actions.

Perception-Action Matching in Joint Action

Perception-action matching in joint action has mainly been investigated in settings that involve conversation. This research shows that perception-action matching leads people to produce similar behaviors even when such similarity is not an explicit goal of the interaction. For example, people tend to mimic the actions of their conversation partners: they are more likely to produce foot shaking movements when they converse with a partner who shakes his or her foot than when they converse with a partner who rubs his or her face (Chartrand & Bargh, 1999). Participants are not aware of this tendency to mimic; it is thought to occur because observing a partner's actions activates representations of those actions, which are then manifest as overt imitation. This manifestation of perception-action matching may benefit joint action indirectly by increasing interpersonal affiliation. People whose actions are mimicked during conversation report liking their conversation partner more (Chartrand & Bargh, 1999) and are more likely to help their partner (van Baaren, Holland, Kawakami & van Knippenberg, 2004) than people whose actions have not been mimicked. Thus perception-action matching may not only support joint action directly by facilitating action coordination but also benefit joint action indirectly by moderating the relationship between coactors.

Action Simulation

The findings reviewed so far indicate that perception-action matching can support joint action by inducing people to produce similar or complementary actions. Perception-action matching can also support joint action in a second way. Once a perceived action or actor-object relation is matched to an action in the perceiver's action repertoire, the perceiver can use his or her own motor system to generate predictions about how that action will unfold (Sebanz & Knoblich, 2009; Wilson & Knoblich, 2005). This process, referred to as action simulation, uses the same internal forward models that predict the sensory consequences of one's own actions (Miall

& Wolpert, 1996) to predict the consequences of other people's actions (Wolpert, Doya & Kawato, 2003). Action simulation typically occurs during action observation but can also be triggered by knowledge about an upcoming action (Kilner et al., 2004).

Evidence that one's own action repertoire can be used to generate predictions about others' actions comes from studies showing that experience in producing an action enhances people's ability to predict the outcome of similar actions. Professional basketball players are better able to predict whether or not an observed basketball shot will be successful than are sports journalists, who have extensive experience observing, but not producing, basketball shots (Aglioti, Cesari, Romani & Urgesi, 2008). Similarly, people are better able to predict the outcome of actions they themselves have produced than actions produced by others. For example, people are better able to predict where a dart will land when they watch videos of their own throwing movements than when they watch others' throwing movements (Knoblich & Flach, 2001). Thus the more similar an action is to the observer's action repertoire, the more accurately its outcome can be predicted.

Action Simulation in Joint Action

Action simulation can support joint action in several ways. First, simulation may allow people to make predictions about their coactors' upcoming actions and modify their own actions accordingly. Becchio and colleagues asked participants to move an object from one location to another in two conditions (Becchio, Sartori, Bulgheroni & Castiello, 2008). The end location was exactly the same in both conditions, except that it took the form of another person's hand in one condition and of a hand-shaped pad in the other. Participants produced different movement trajectories in the two conditions; the object was approached more slowly, with a smaller grip aperture, and was also placed in its end location more slowly, when the end location was another person's hand. Thus participants handled the object in a way that made it easier for the other person to grasp it in the joint action condition. This suggests that participants may have simulated the other person's upcoming action (grasping the object) and modified their own action kinematics accordingly.

Second, action simulation guides attention during joint action. Welsh and colleagues asked pairs of participants to sit across from each other and detect targets that appeared on a screen in between them (Welsh et al., 2005). When people perform a target detection task alone, they are slower to detect targets that appear in the same location as an immediately pre-

ceding target, a phenomenon known as inhibition of return. Welsh and colleagues showed that inhibition of return also occurred when participants were asked to detect a target to which they had just watched their coactor respond. This suggests that people simulated their partner's action, which led to similar inhibition of attention toward their partner's location as if they had responded to that location themselves. This effect also occurred when the participants could see the effect of the partner's response (i.e., the illumination of a response button) but not the partner's movements, indicating that knowledge of the partner's action was sufficient to induce simulation (Welsh, Lyons, et al., 2007). Flanagan and Johansson (2003) tracked participants' eye movements as they stacked a series of blocks and as they watched another person stack the blocks. When people move objects themselves, their eyes make predictive movements toward upcoming objects and locations rather than reactive movements following the motion of the objects. In the observation condition, participants' eye movements showed this same pattern of predictive eye movements, suggesting that the participants simulated the observed actor's movements and were thus able to attend to the objects they expected to be manipulated next. Thus predictive action simulation may guide the allocation of attention during joint action.

Third, action simulation may support temporal coordination between multiple performers in two ways. First, in tasks such as ensemble music performance that require performers to produce independent yet coordinated actions, each performer may run parallel simulations of both their own and their partners' actions. In support of this hypothesis, Keller, Knoblich, and Repp (2007) showed that pianists were better able to synchronize one part of a duet with a second part that was recorded months earlier by themselves than by another performer. This suggests that they may have relied on internal models to predict the timing of their own duet part and the part they synchronized with, and this prediction was most successful when the part they synchronized with closely matched their own (in this case, because it was their own earlier action). Converging evidence for this hypothesis comes from a study of duet performance that showed that pianists are better able to coordinate with partners to whom they are more similar in terms of preferred performance rate (Loehr & Palmer, 2011).

Second, in tasks that require performers to produce events jointly rather than independently, coperformers may generate predictions about the temporal consequences of their combined actions rather than separate predictions for each person's actions. To test this hypothesis, pairs of participants

were asked to track a moving target on a computer screen (Knoblich & Jordan, 2003). One participant controlled the key that decelerated the tracker, and the other controlled the key that accelerated it. After training during which participants had access to feedback concerning the timing of each other's keypresses, pairs of participants were just as good at performing the task as individual participants who controlled both keys. These findings suggest that with training, participants were able to generate predictions about the timing of their combined actions and use these predictions for effective coordination.

Finally, action simulation may be modulated by the relationships between interaction partners. Kourtis and colleagues asked groups of three participants to take turns lifting an object (Kourtis, Sebanz & Knoblich, 2010). EEG was recorded from one participant, who gave the object to one member of the group (the interaction partner) on some trials but never interacted with the other group member (the loner). Each group member lifted the object alone on some trials. Participants' anticipatory motor activity, reflecting simulation of another group member's upcoming action, was stronger when they expected their interaction partner to lift the object alone than when they expected the loner to lift the object alone. Thus the degree to which participants simulated others' actions depended on their social relationship to the observed actor.

In sum, perception-action matching supports joint action in two ways. Matching an observed action onto one's own motor system can facilitate production of that same action or a complementary action, depending on the goals of the actor and the observer. This process can lead interaction partners to produce matching behaviors, as evident in nonconscious mimicry during conversation, and may indirectly benefit joint action by increasing interpersonal affiliation. Matching an observed action onto one's own motor system also allows predictions to be generated about unfolding actions. This predictive action simulation allows people to modify their actions in relation to others' actions, guides people's attention during joint action, and helps people predict when a partner will act in order to align the individual components of joint actions in time.

It is important to remember that close links between perception and action can lead to emergent coordination whether people plan to coordinate with each other or not. These links also support planned joint action such as music performance, in which two or more people intend to coordinate their behavior. However, planned joint action also requires mental representations and processes that go beyond the perception-action links discussed in this section. We turn to these processes next.

Shared Representations and Perceptions

Shared representations of the desired outcome of joint action, as well as each person's part in achieving that outcome, can support joint action even in the absence of direct perception of a partner's actions. These representations may specify the particular actions the coactor must produce or the task rules under which the coactor operates, and can be used to guide action planning, monitoring, and control (Vesper et al., 2010). People engaged in joint action may also incorporate their partners' perceptions into their representations of the task by taking a partner's perspective or by inferring what the partner can and cannot perceive (Samson, Apperly, Braithwaite, Andrews & Bodley Scott, 2010). This too can facilitate monitoring of, and adaptation to, a partner's actions. We describe each of these processes in turn.

Shared Task Representations

In ensemble performance of Western music, each performer's part is commonly specified in advance in a musical score. The pianist and violinist in our earlier example would have used the score to learn their individual parts and how they relate to each other to form a musical whole (Keller, 2008). They may also have used the score to learn the details of each other's parts. This musical example illustrates the representations that may be shared in planned joint action. Each person must minimally represent his own part in the joint action (the pianist's part), as well as the desired joint outcome (the musical piece), and there must be some awareness that the joint outcome cannot be achieved alone (Vesper et al., 2010). Each person may also represent his coperformer's part in the joint action (the violinist's part), though this is not always necessary for successful joint action. For example, the pianist may simply represent her own part in the musical performance and have the goal of remaining temporally coordinated with the violinist. However, people often form representations of each other's tasks during joint action when doing so is not necessary for, or is even detrimental to, performance (Sebanz, Knoblich & Prinz, 2003; Tsai, Kuo, Jing, Hung & Tzeng, 2006). These representations of a coactor's task modulate each person's action planning, control, and monitoring.

Action Planning

The first evidence that representations of a coactor's task influence action planning came from studies that examined joint performance of a Simon task (Sebanz et al., 2003; Sebanz, Knoblich & Prinz, 2005). When participants

perform a Simon task alone, they are required to produce one of two action alternatives, such as a left or right button press, in response to a stimulus, such as the color of a ring on a finger. A stimulus feature that is irrelevant to the task, such as the pointing direction of the finger, induces a response conflict if it is spatially incompatible with the required response. For example, participants are slower to respond to a red ring with a right button press if the ring sits on a finger that points to the left (in the direction of the alternative response). In the joint Simon task, the two action alternatives are distributed between two people, and spatial incompatibility effects are still observed: participants are slower to respond to a red ring with a right button press if the ring sits on a finger that points to the left, even when it is the coactor rather than the participant himself who is responsible for left button presses. No such effects are observed when participants perform their half of the task alone (i.e., when participants are responsible for the right button press, and no one is responsible for the left button press). Thus participants in the joint Simon task form representations of their coactor's task, which influence their own action planning (in this case, response selection).

Shared representations influence action planning even in the absence of direct perception of the coactor's actions. The spatial compatibility effects observed in the joint Simon task also occur when participants merely believe that another person is responsible for the second action alternative (Ruys & Aarts, 2010; Tsai, Kuo, Hung & Tzeng, 2008; but see Welsh, Higgins, Ray & Weeks, 2007, for different findings). This suggests that participants' action planning is constrained by representations of their partners' tasks formed in advance of the joint action. Furthermore, there need not be overlap between the spatial features of the stimulus and the coactors' responses in order for a partner's task to influence action planning. Rather, participants represent the arbitrary task rules that govern their coactors' behavior (Atmaca, Sebanz & Knoblich, 2011; Ramnani & Miall, 2004; Sebanz, Knoblich & Prinz, 2005). For example, Ramnani and Miall (2004) trained pairs of participants to produce finger movements in response to arbitrary visual stimuli (shapes) whose color determined which participant should respond. The brain activity of one member of the pair was then measured using fMRI while he or she performed the task under the belief that the other member of the pair performed the task outside the scanner. Stimuli to which the coactor was meant to respond yielded preparatory motor activity in the scanned participant, indicating that the arbitrary task rules under which the coactor responded activated motor

representations in the scanned participant. Thus corepresentation of arbitrary task rules influences action planning during joint action.

Action Control and Monitoring

Shared task representations also influence action control. Evidence for this comes from EEG recordings of participants' brain activity while they performed the Simon task described in the previous section (Sebanz, Knoblich, Prinz & Wascher, 2006; Tsai et al., 2008). Recall that in the joint Simon task, participants respond to one stimulus color, while the coactor responds to the other stimulus color. Thus the participant must not respond when it is the coactor's turn to do so; trials of this type are referred to as no-go trials. Participants can also perform this task individually: they can respond to one stimulus color but not the other, with no coactor involved. No-go trials can then be compared under conditions in which the stimulus refers to a coactor's task (joint condition) and in which the stimulus refers to no one's task (individual condition). EEG activity measured during no-go trials reveals a more pronounced positive event-related potential 300–500 ms after the stimulus in the joint condition compared to the individual condition (Sebanz, Knoblich, et al., 2006). This ERP component is thought to reflect action inhibition, which is stronger when it is the coactor's turn to act than when it is no one's turn to act. Thus this finding indicates that corepresentation leads participants to recruit action control processes to ensure that they do not act when it is the coactor's turn to do so.

Representations of a coactor's task also govern action monitoring. Schuch and Tipper (2007) investigated action monitoring and control by having participants perform a stop signal task with a coactor. In stop signal tasks, people are required to respond to a target as quickly as possible. On some trials, they must stop the response when a stop signal is presented shortly after the target. The timing of the stop signal is manipulated so that participants sometimes successfully stop the response (engaging inhibitory processes) and sometimes cannot stop the response (producing errors). When people perform this task alone, they are typically slower at responding to the target that immediately follows the stop signal, both when they inhibited the previous action and when they made an error. These same aftereffects are evident when participants respond to a target after observing a coactor successfully inhibit their action or make an error. Thus participants monitor their partners' actions for errors, which affect participants' performance just as their own errors do; similarly, a partner's action inhibition elicits similar inhibitory mechanisms in one's own actions.

Shared task representations can also influence multisensory integration. In a recent study, participants were asked to judge the location of a tactile stimulus that was presented on the top or bottom of a foam cube that they held with both hands (Heed, Habets, Sebanz & Knoblich, 2010). When participants perform this task alone, visual distractors (lights) that are presented at the elevation opposite to the tactile stimulation (top versus bottom of the cube) reduce the speed and accuracy with which participants judge the location of the tactile stimulus, indicating interference between the two modalities (Spence, Pavani & Driver, 2004). However, when participants performed the same task with a coactor who responded to the location of the visual distractors, this cross-modal interference was reduced. In other words, participants were better able to ignore the distractors when another participant responded to them. This finding suggests that corepresentation may facilitate rather than interfere with task performance when coactors respond to stimuli from different sensory modalities. However, this facilitation occurred only when the coactor sat within the participant's peripersonal space, indicating that corepresentation effects may differ depending on the spatial relationship between coactors (for related findings, see Guagano, Rusconi & Umiltà, 2010; Welsh, 2009).

Social Context

Finally, the tendency to share representations with a coactor may be modulated by the social context of the interaction and the characteristics of the coactors. Iani and colleagues found typical corepresentation effects in the joint Simon task in a cooperative, but not in a competitive, context (Iani, Anelli, Nicoletti, Arcuri & Rubichi, 2011). Hommel and colleagues found the joint Simon effect when the participants' coactor was friendly and cooperative, but not when the coactor was competitive and intimidating (Hommel, Colzato & van den Wildenberg, 2009). Kuhbandner, Pekrun, and Maier (2010) found corepresentation effects after participants watched movies that induced a positive or neutral mood, but not after they watched movies that induced a negative mood. Thus a negative relationship with the coactor or a negative mood reduces people's tendency to corepresent their partners' actions. The ability to infer others' mental states may also influence corepresentation. Ruys and Aarts (2010) used the "mind in the eyes" test, in which participants judged the emotional state of pairs of eyes, to determine participants' ability to infer mental states. Those who were less able to infer others' mental states only showed corepresentation in a competitive context, whereas those who were better able to infer others' mental states showed corepresentation effects in both competitive and

cooperative contexts. In line with this finding, neurological patients with impairments in mental state attribution do not show the joint Simon effect, unless they are explicitly instructed to pay attention to their coactor (Humphreys & Bedford, 2011). However, Sebanz, Knoblich, Stumpf, and Prinz (2005) found similar corepresentation effects in a group of high-functioning individuals with autism and a matched control group of adolescents and adults, suggesting that deficits in understanding others' mental states do not necessarily preclude corepresentation.

In sum, shared representations of coactors' tasks are formed even when they are not necessary for successful performance of a joint task, and even though they sometimes interfere with performance of individual tasks. Shared task representations can arise without visual access to the coactor's actions, suggesting that advance knowledge of a coactor's task can become incorporated into one's own action plans. Shared task representations influence not only action planning but also action control and stimulus processing, though these effects may be modulated by the social context of the joint action. Overall, then, people engaged in joint actions take their coactors' tasks into account when producing their own actions. Can the same be said for their coactors' perceptions?

Shared Perceptions

Joint action is supported by people's ability to assess what their coactors can and cannot perceive. In duet music performance, both performers attend to the overall sound to ensure that they produce a cohesive performance (Keller, 2008). The performers also rely on shared perceptual cues that both attend to at key moments for temporal coordination (Williamon & Davidson, 2002). In other situations, people engaged in joint action may have access to the same perceptual information but from different perspectives, such as when two people perform a task while sitting on opposite sides of a table. In this case, they may take each other's perspectives when performing the joint action by mentally rotating themselves into each other's orientation (Kessler & Thomson, 2010) or by switching from an egocentric to an allocentric perspective that allows for an agent-neutral view on shared visual stimuli (Böckler, Knoblich & Sebanz, 2011). People engaged in joint action may also have access to different perceptual information, in which case they may infer what their coactors can and cannot perceive. Sharing perceptions with a coactor, whether through joint attention, perspective taking, or inference, facilitates coordination by allowing people to modify their own actions according to what their partner perceives.

Shared Perceptual Cues

In music performance, performers can attend to both their own part in the performance and the jointly produced performance. Keller (2005) asked drummers to perform one rhythm while a computer simultaneously produced a different rhythm, in which the performer's rhythm was embedded. The drummers were able to subsequently reproduce the computer's rhythm, indicating that they attended to the aggregate rhythm in addition to their own embedded rhythm. However, musicians do not always have access to auditory feedback from each other's actions. In this case, visual cues may be used to guide attention. Williamon and Davidson (2002) recorded duet pianists' practice sessions and showed that with practice, the pianists increasingly relied on eye contact to guide coordination when one or both performers had not yet begun to play. Goebl and Palmer (2009) showed that visual information about a given performer's movements (the height to which fingers were raised above the keys) was exaggerated when the coperformer did not have access to auditory feedback from the performance. These findings suggest that different perceptual cues may be used to draw a coperformer's attention, and thus facilitate coordination, depending on the sensory information available to each performer.

In the visual domain, being able to assess what a partner can perceive facilitates performance of joint tasks. Brennan and colleagues asked pairs of participants to perform a joint visual search task (e.g., looking for the letter *O* in an array of *Q*s). They compared performance in a condition in which partners shared information about where each of them searched the display (through cursors indicating each person's gaze location) with a condition in which partners could only communicate verbally. Performance was faster when partners could perceive each other's gaze. In the shared-gaze condition, pairs were better able to distribute the search task between themselves (Brennan, Chen, Dickinson, Neider & Zelinsky, 2008), and they used gaze to communicate the target location instead of relying on verbal communication (Neider, Chen, Dickinson, Brennan & Zelinsky, 2010). Thus assessing the location of a partner's attention can facilitate coordination in joint action.

Perspective-Taking

People engaged in joint action may share access to the same visual information but from different perspectives. Recent evidence suggests that people may take their partner's perspective into account in such situations. When one person mentally rotates an image while a partner looks at the same image, the person is slower to perform a small rotation (large rotation

from the partner's perspective) and faster to perform a large rotation (small rotation from the partner's perspective) compared to when the partner is not looking at the image (Böckler, Knoblich & Sebanz, 2011). This suggests that engaging in joint attention from different perspectives triggers a switch from an egocentric perspective to an allocentric, agent-neutral perspective. People may also compute another person's perspective when that perspective contains perceptual information different from their own. Samson and colleagues (2010) asked participants to judge their own or another person's visual perspective (to indicate how many discs, hanging on a virtual wall, could be seen by them or by a computer avatar). People were slower to judge their own perspective when the other person's perspective contained different information (a different number of discs) than their own perspective. Thus participants computed the avatar's perspective even though doing so was detrimental to their own performance. This parallels the findings on task corepresentation, which occurs even in circumstances where taking another's task into account interferes with one's own performance.

In sum, sharing perceptions with a coperformer facilitates coordination in several ways. Providing a jointly attended perceptual cue to a partner facilitates the temporal alignment of actions in tasks such as music performance. Being able to assess what a partner can perceive allows for more efficient communication and task distribution. When partners have different perspectives on the same visual information, they may automatically compute each other's perspective; computing another's perspective may occur even when coactors have access to different perceptual information. Sharing perceptions and attention with a partner is thus an important component in understanding joint action.

Conclusion

The two musicians who performed a duet at the beginning of this chapter relied on several processes to achieve their joint performance goals. Shared representations and perceptions of their own, their partner's, and their combined tasks governed how the performers planned and monitored their own actions and monitored each other's actions. At the same time, close links between the two performers' actions and perceptions allowed them to coordinate their actions precisely in time and to make predictions about their partner's actions as they unfolded. Neither perception-action links nor shared representations alone can explain how the pianists performed their duet. For example, shared representations defining the actions

each performer should produce are not sufficient to guarantee that those actions will be aligned in time. Likewise, coupling between perceptions and actions is not sufficient to specify who should perform which actions to bring about a joint outcome. Both of these elements are important for the musicians' successful performance; how processes related to perception-action coupling and shared representations work together during duet performance and other joint actions remains a question for future research. Nevertheless it is clear that the actions and perceptions of the pianist cannot be fully understood without considering the actions and perceptions of the violinist. Given the common occurrence of joint action in everyday life, neither can any individual's actions and perceptions be fully understood without considering the actions and perceptions of those with whom he or she interacts.

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VI Cognition and Volition

14 Premotor or Ideomotor: How Does the Experience of Action Come About?

Valerian Chambon and Patrick Haggard

Introduction

The sense of agency refers to the experience of controlling one's own actions and their external effects. We normally feel in control of our actions, and perhaps also of our lives more generally. Therefore the sense of agency is as much a backdrop to our normal mental life as a distinctive phenomenal experience. Indeed, sense of agency only really becomes apparent as a sense of *nonagency* when the normal flow from our intentions to the effects of our actions is broken. Clearly, if disruption of agency occurs from breaks in the intention-action-effect chain, then the normal sense of agency must arise somewhere along this chain. But where? This is the question of this chapter. Capturing where the sense of agency comes about requires specifying this chain properly. In particular, the account must explain how we can sometimes be deluded about our own agency. At the same time, it must also explain why we are not deluded all the time.

Most studies on agency are embedded in the theoretical framework of the ideomotor theory (IM). IM is a theory about the psychological representation of actions. Essentially it holds that the key mental representation of actions happens in terms of the effects of action in the outside world. Critically, it is taken to imply that the detailed motor commands and means used to achieve those effects are not psychologically available but are specified by dedicated modules at lower control levels. An important corollary of IM is that the intention to perform action becomes essentially the same thing as the mental representation of that action's effects. In the standard and still-influential formulation of IM by William James (1890/1950), "Whenever movement follows unhesitatingly and immediately the notion of it in the mind, we have ideo-motor action."

IM theory therefore focuses on the bounding elements of the intention-action-effect chain. More specifically, it emphasizes the direct and immediate

link between intention and effect at the expense of the mechanisms of action itself. Motor control becomes the "excluded middle" of ideomotor theory.

In this chapter, we tackle the problems of excluding intermediate stages along the chain. We consider the recent emphasis on comparator models for action attribution and investigate whether or not these models add an important intermediate stage to theories of action representation, and thus go beyond IM. Next we consider the process of action selection itself, which has largely been ignored in discussions of IM. The action selection stage is crucial to account for how action effects are *causally* related to intentions. We suggest that action selection processes must be reincorporated in the phenomenology of action, and IM theory cannot readily do this. We present experimental evidence showing that signals arising from the workings of these processes may indeed affect how actions and effects are experienced. Signals linked to action selection processes may prospectively inform later, retrospective judgments of agency. Therefore we identify an important gap in ideomotor theories of action: they do not sufficiently recognize *pre*motor processes. In the final section, we consider the relation between action selection and responsibility. We note that the IM theory's failure to emphasize action selection processes leads to difficulties in attributing responsibility.

The Ideomotor Theory

The Ideomotor Causation of Action

Agency is a key component of action experience. In a nutshell, agency refers to the sense of controlling one's own actions and, through these actions, events in the outside world. We rarely have an intense, clear phenomenology of agency, but we clearly recognize failures of agency when we experience actions that do not unfold as expected or fail to produce intended effects. One might even say that our sense of "authorship" becomes apparent only when it is *falsified*, resulting in a break of the flow from intentions to action effects that normally characterize experience. Thus, determining where action experience comes from requires properly specifying where the break may occur along the intention-action-effect chain. Identifying the break may in turn depend on how we choose to specify the chain, and on the causal relation between its constituents.

The ideomotor (IM) theory is a strong theory about what this causal relation is. First coined by Carpenter in 1852, the term "ideomotor action"

was brought to the attention of psychologists by Hermann Lotze in continental Europe, and by Henry James at the end of the nineteenth century (Lotze, 1852; James, 1890/1950). In its earlier developments, the IM theory was an attempt to solve the problem of how our voluntary actions come about. James's suggestion was that a movement can be considered voluntary when no intermediate operations come between the intention to act (the "idea") and the action itself. An immediate translation from ideas to movements is thus required to capture the true essence of what a voluntary action is, that is, an action that follows "unhesitatingly and immediately the notion of it in the mind" or "the mere thought of it" (James, 1890/1950, p. 522). This direct relation between the action and its idea is here a consequence of their *similarity of content*. In James's view, a voluntary action is essentially represented by its perceivable effects. Thus, thinking of the effect—anticipating the effect in mind—is sufficient to activate *immediately* the corresponding action. A voluntary action is therefore *ideomotor* in nature: it is an automatic expression of an idea dominant in our minds at the time, rather than a movement prompted by a distinct volitional effort (Carpenter, 1874, p. 280; see Greenwald, 1970, for a similar modern claim).

The IM account of voluntary action makes a strong argument against the "homunculus argument" and the associated regress problem. That is, to explain how action comes about, James's IM theory does not need to presuppose any intervening mental operation (such as a will) or any additional mental antecedent. Voluntary actions are triggered by merely thinking of their effect, and this thought is sufficient to evoke a muscular movement. In other terms, the *expectation* of a result is by itself sufficient to trigger an action. The notion of "internal volition" is eliminated in favor of a mental representation of the end state that bears the causal efficiency of the whole intention-effect chain. A "conscious" intent is no longer a necessary antecedent of voluntary action (see also Carpenter, 1852; Hommel, 2007a).

In James's IM theory, the similarity of content between an action's idea and an action's effect assumes a particular causal link between the agent's intention and the outcomes of the forthcoming action. Because intended and perceived outcomes of an action are similar in content, one should be able to predict a relational symmetry between action and perception. In action, activating the mental image of the external effect should trigger the corresponding action automatically, just as in perception, exposure of an external event triggers a mental image (see Shin, Proctor & Capaldi, 2010, for review). Put another way, a mental image of the to-be-produced effect (endogenous trigger) should be sufficient to initiate an action, and

conversely, perceptual events (exogenous triggers) should be sufficient to generate actions for which the feedback is similar. *Reciprocity* and *immediacy of causation* between an action's idea and its effects directly follow from their similarity of content.

Taken together, James's ideomotor principle and its later versions (see Prinz, 1987; Knuf, Aschersleben & Prinz, 2001) have a number of consequences for how we define the intention-action-effect chain and, more specifically, for the role that the action itself plays in this chain. The IM theory specifies that any intermediate steps between "late" products of action processing (the external effect of an action) and "early" cognitive antecedents of action (mental image of the external effect) are irrelevant. As a consequence, internal processes of action preparation, selection, and control—that is, intermediate processes by which an intention is converted into action—are bypassed or downplayed.

As suggested earlier, this downplaying of intermediate action processes is a direct consequence of the ideomotor account of action causality. In a sense, the selection process is externalized in, and completed by, mere anticipation of the effect itself. There is no internal "pondering" or elaboration process. This is why the ideomotor compatibility effect[1] is not affected by increasing the number of competing responses or stimulus-response alternatives (Wright, Marino, Belovsky & Chubb, 2007), in contrast to the classic findings in most action selection tasks (Hick, 1952). Selecting an appropriate response or an appropriate task set from a range of alternatives is a key operation of cognitive control (Koechlin, Ody & Kouneiher, 2003; Barbalat, Chambon, Franck, Koechlin & Farrer, 2009). In contrast, IM theory begins from the point where selection and control end: once the external effect of an action has been mentally represented, IM theory does not have any further place for action selection processes, because the action itself must automatically follow.

The two main features of the IM theory—similarity of content and immediacy of causation—necessarily call for a compression of the intention-action-effect chain into a single, unique link, directly articulating the idea of the external effect (the intended outcome) with the production of the external effect itself (the perceived outcome). This naturally has consequences for how we *experience* action and, more generally, for specifying where this experience comes about. According to IM, the only information that is consciously available regarding the action is the representation of the subsequent effect (Hommel, Müsseler, Aschersleben & Prinz, 2001; Jeannerod, 2006). Action experience is therefore limited to perceptual representations of action outcomes, with intermediate action selection and

guidance processes residing beneath the horizon of consciousness (see Lynn, Berger, Riddle & Morsella, 2010; Gray, 2004; Libet, 2004). Considering the action as a vanishing intermediary between intention and effect thus led ideomotor accounts of agency to uphold the seemingly paradoxical claim that to account for action experience, action itself is irrelevant.

The Ideomotor Account of Action Experience: The Vanishing Action

If the workings of motor programs are beyond conscious access, then action experience cannot come about from the action unfolding itself but instead comes from external monitoring of action outcomes. In this view, attribution of agency is merely post hoc: it is done offline, after the intention-action-effect chain is completed and after action effects are known. As we see it, this retrospective account of agency is a direct consequence of two major ideomotor principles:

1. *Immediacy of causation*. The causation of action from intention is direct: no intermediate steps are required for motor transformation from the idea behind the action's inception. Therefore what happens at time of action selection is irrelevant for action experience.
2. *Similarity of content*. If there is no output from action to action experience, then one can just retrospectively check that action effects resemble their causative images. One feels in control if, and only if, the effect image has been properly externalized in outcomes the image predicts—i.e., if there is a match between intended and perceived action effects.

The IM intention-effect chain is here supplied with a purely associative, general sense-making mechanism. This mechanism makes retrospective assumptions about what happened during the unfolding of action, based on similarity of content between intended and perceived action outcomes. According to the IM view, action experience is based only on outputs of this retrospective mechanism for evaluating whether actions do or do not achieve anticipated effects. This retrospective, association-based account of action experience is directly inspired by Hume's understanding of causality. We do not have any insight into the nature of the "power" or force connecting two events, but we may infer from two events co-occurring that a connection must underpin their conjunction (Hume, 1740/1978).[2] Causal relationships between events are assumed, rather than *perceived* or *known*, by retrospectively noticing constant conjunctions between those events. Likewise, causal efficiency of our actions on the outside world is deduced by noticing co-occurrences between what we intended to do and what we eventually get, as an action effect (fig. 14.1). In the IM account

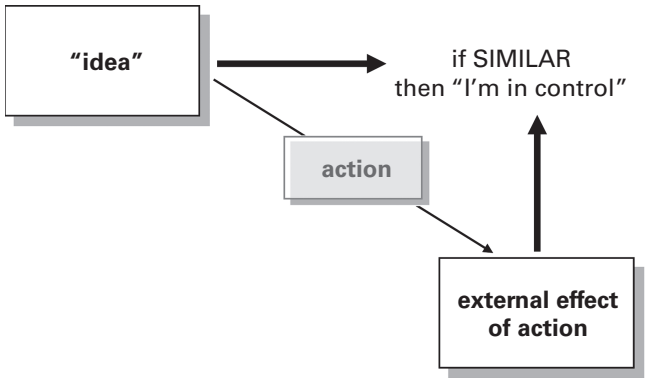

Figure 14.1
Standard IM account of action experience. "Idea" or image of the effect triggers an action whose feedback is similar to this image; conversely, a stimulus triggers an action whose effect resembles this stimulus. Agency is inferred retrospectively by noticing *perceptual conjunctions* (e.g., similarity) between action's idea and action's effect.

of action experience, the causal efficiency of our actions is therefore inferred by assuming, rather than *experiencing*, a causal path between intention and effect (see Wegner, 2003).

Most studies of retrospective agency are (explicitly or not) embedded in the theoretical framework of James's ideomotor principles and, to some extent, their modern developments. In this account, as we just saw, action experience is a purely mental construct, being retrospectively inferred after the action is done. Retrospective attribution of agency serves to explain one's own behavior and could therefore be useful in making sense of internal and external events (Metcalfe & Greene, 2007).

Because agency is confined to a retrospective reflection based on general information about the environment, attribution of agency is therefore subject to errors and approximations. Such errors can be induced artificially by fooling underlying ideomotor mechanisms, either by directly increasing predictive representation of the effect (e.g., by showing the effects of an action as a prime before the action itself; see Aarts, Custers & Wegner, 2005; Linser & Goschke, 2007; Sato, 2009) or by creating opportunistic conjunctions between a participant's intention and external outcomes (Wegner, 2002, 2003).

So far, most experimental inductions of (deluded) agency have been obtained by varying the consistency between prior thought and outcome

(Wegner, 2002; see also Dijksterhuis, Preston, Wegner & Aarts, 2008). For example, it has been shown that people feel in control when they have a conscious goal in advance of the action (such as to do well on a task) and when the outcomes of a series of movements match what they initially intended to do (Knoblich & Sebanz, 2005). Similarly, Wegner, Sparrow, and Winerman (2004) showed that hearing instructions in advance resulted in participants expressing a greater feeling of control over the movement of someone else's hands, compared to not hearing instructions in advance. In the same vein, if a volunteer finds her hand moving shortly after having the thought of moving it, then she is prone to believe that she initiated the movement herself although the movement was actually caused by someone else (Wegner & Wheatley, 1999). More generally, manipulation of prior thought can lead one to believe that one intended to do something that one did not in fact intend (Wegner, 2003; Lynn et al., 2010; Banks & Isham, 2009).

Delusions of agency through fine experimental manipulations work because, according to the IM theory, action experience cannot be predicated on mechanisms underlying unfolding actions and motor control. And it works because action experience is, and is only, the output of a post hoc, high-level cognitive process that reconstructs experience offline from the perception of lawful correspondences between action intentions and action outcomes (Banks & Isham, 2009; Wegner, 2002, 2003). Accordingly, the IM account of action experience explains why we can occasionally be deluded by coincidental intention-effect matches. However, it fails to account for why we are not deluded *all the time*. To justify its relevance in describing the phenomenology of action, IM theory needs to provide a mechanistic explanation for why our sense of control is not fooled by *any* conjunctions between intention and external outcomes.

This could be the central weakness of IM-based theories of agency. Ideally, any action theory should be able to generate a satisfying, if not exhaustive, account of action experience, including providing such a mechanistic explanation of why and how we are prevented from constant delusions of agency. IM theory, however, is a theory of intentional (and perceptual) induction of voluntary behavior rather than a genuine theory of action. It poorly specifies the intention-action-effect chain and is not sufficiently explicit about the mechanisms by which effective causality is driven along this chain—that is, by which (intermediate) processes an idea can be converted to action (Kunde, 2001; Shin et al., 2010; but see Jeannerod, 2001). Thus, by leaving unspecified what happens at time of action selection, IM theory is paradoxically unable to account for pathological

conditions in which ideomotor mechanisms are disrupted. In ideomotor apraxia, patients are able to understand what to do but often fail to translate the idea into physical action, even with intact motor abilities (Halsband, 1998). If ideomotor theory were true, then "when one knows what to do with intact motor skill, planning of action should be converted into action seamlessly" (Shin et al., 2010, p. 969). Patients' failure to make this conversion implies that a certain extra bridge is required to be intact to translate idea to action. So far, we can suggest that selecting the appropriate action is a key element in this bridge, and that IM theory does not provide a convincing explanation for it.

Ideomotor Theory and Computational Models of Motor Control

We have seen that IM theory downplays the intermediate mechanisms that translate intentions into actions and thus produce their effects. In this respect, IM theory seems profoundly at odds with recent work in computational motor control. This field has recently made significant progress through providing explicit computational models of intermediate mechanisms that link intentions to effects. In this section, we consider the implications of predictive forward models (also known as "comparator" models) for IM theory. The discussion is based on the predictive forward model of Frith, Blakemore, and Wolpert (2000).

The predictive forward model begins with a desired goal state. First, the goal state is fed to a planner, or inverse model, which selects appropriate motor commands to achieve the goal. These commands are then executed by sending them from the brain to the musculature. At the same time, a copy of the motor commands ("efference copy") is fed to a forward model, which predicts the effects of the motor commands. Thus, to the extent that the forward model is accurate, the control system has access to information about the state of the body in advance of delayed sensory feedback from the body itself. This predictive information can then be used in two critical comparisons. First, it can be compared to the desired goal state to assess whether further motor commands are required or whether the action has achieved its goal. Second, more importantly for our purposes, it can be compared to sensory information about effects of action. This second comparison assesses whether sensory information is or is not a predicted consequence of the current motor command. It can thus be used to distinguish sensory events that are self-caused (reafferences) from those that are independent of the self (exafferences). In the original formulations, the forward model predicted low-level kinematic features, such as hand posi-

tion during reaching movement. However, the framework can readily be extended to include predictions about external effects of action, including sensory effects. Thus predictive forward models elegantly explain why you cannot tickle yourself (Blakemore, Wolpert & Frith, 1998, 2000). As mentioned earlier, an intentional (i.e., self-produced) action is generated together with its own "image" (the efference copy). This offline copy can be used to predict the subsequent sensory effects of the action. When the prediction is accurate, these sensory effects are attenuated, resulting in a decreased ticklishness of self-produced tactile stimulation (Blakemore et al., 2000). Conversely, a discrepancy between predicted and actual sensory feedback leads to less sensory attenuation and an increase in ticklishness.

In summary, the forward predictive models provide a clear theory of the control of skilled actions. They also provide a clear theory of the intentions and action effects: action effects are precisely those sensory events that can be predicted from one's intentions, using the specific intermediate mechanism of the forward model. By providing an explicit intermediate mechanism, these models seem to solve one of the major difficulties of the IM model. As we outlined earlier, IM models are prone to infer agency based on spurious correlations between intentions and action effects. The predictive forward model assesses agency not by correlating events but by checking parameter values. This more detailed information should be more robust to opportunistic correlations. Thus a prediction/comparison mechanism may explain better than IM theory why we are deluded only rarely, as opposed to frequently.

At the same time, we may question whether the forward model is really a strong alternative to IM theory or merely a new version of it. The point essentially turns on where we locate intentions within this model. This is an issue of considerable terminological confusion, given that (a) the term "intention" does not figure directly in the computational modeling literature, and (b) the term is used in a number of different senses in the philosophical and psychological literatures (Pacherie, 2000; Chambon et al., 2011). For example, intentions are sometimes defined with respect to simple motor goals (i.e., goals that can be realized by basic actions such as lifting an arm, pressing a button, or reaching for an object). According to this definition, intentions are sensorimotor representations where the goal is represented directly in terms of the motor commands needed to achieve it. But intentions can also be defined as higher-order goals (e.g., quenching one's thirst), the achievement of which may involve the completion of a number of motoric subgoals (e.g., grasping a glass, opening a tap, filling the glass, closing the tap, etc.). Crucially, these higher-order intentions

include a future-directed component and do not contain any reference to the practical *means* required to achieve them (Pacherie, 2000). They are also formed upstream to the action specification process. In contrast, basic intentions can be seen as *being* the action specification process, since they guide the action in real time. Thus the meaning of "intention" clearly depends on which stages of the action specification process are being discussed. Some of the functions attributed to intentions are typically played in the period between the initial formation of the intention and the initiation of the action ("upstream" intention). In contrast, other functions—in particular, their role in guiding and monitoring the action—are played in the period between the initiation of the action and its completion ("downstream" intention).[3]

Predictive forward models locate intentions within the action specification process. Therefore it is crucial to assess whether they effectively refine or merely relabel the IM account of action experience. Recall that IM theory is based on the strong similarity between intention and action effect. If we identify intentions with the desired goal states of the predictive forward model (upstream intention), we can see that this model does add genuine mechanistic detail about the intermediate mechanisms between intention and effect representation. In that reading, the forward model certainly breaks the tight correlation or symmetry suggested by IM theory, and would represent a genuine alternative.

Taking another view, one might identify the efference copy of the predictive forward model with intentions (downstream intention). In that case, the intention contains essentially the same information as the action effect, since the intention predicts the action effect. In this reading, the predictive forward model could be seen as a simple relabeling of IM theory rather than a genuine alternative.

The difference between these two views lies in the role of the planner. Recall that the planner is an action selection mechanism: given a goal, it selects the specific means or motor commands required to achieve the goal. As so often in action theory, the means/ends distinction appears crucial. Since IM theory aims to downplay means, it associates intentions in the sense of ends with action effects. Since the predictive forward model aims to explain means, it needs to provide a description of how specific means are selected and monitored. It does this through the planner and the forward model respectively. Whereas in IM theory, intentions have direct and immediate causal efficacy over effects, in the forward model the intermediate steps of action selection and action monitoring ensure the causal chain between intention and effect.

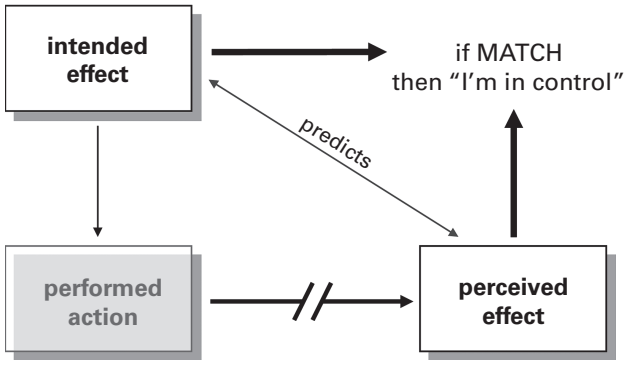

Figure 14.2
Predictive account of action experience. The motor system predicts perceived effects from the intended movement. Sense of control is stronger when a close *match* exists between the intended and the actual (i.e., observed) effects of the action than in the case of a mismatch (broken line).

In this sense, the forward model is effectively a refinement of IM theory. It reintroduces the action along the intention-effect chain to explain how intended and desired effects are linked. Through the mechanism of efference copy monitoring, information about *how* the action unfolds becomes relevant to the sense of control. However, in predictive forward models, action experience is still essentially retrospective, since the match between predicted and actual effects can be made only *after* the action is performed and its consequences are known (fig. 14.2).

A Premotor Contribution to Action Experience

From Intention to Action: The Missing Link

We have argued that action selection processes play an important role in the phenomenology of action, although this role has been neglected by IM theory. In this section, we describe this contribution in more detail and show that it is important for understanding the concept of responsibility for action. We begin with a thought experiment inspired by the notion of the "deviant causal chain" in moral philosophy (Chisholm, 1966). How we define agency has important consequences for issues of legal and moral responsibility—that is, for deciding whether and to what extent one is able to answer for one's actions. In a nutshell, responsibility is about determining whether one's actions are or are not *causally* related to one's intentions; conversely, it is about whether the agent's intention has been embodied

in an action *specifically* meant to achieve the desired effect. This constraint explains both why the normal sense of control is not fooled even though IM requisites are met, and why we are not deluded by every conjunction between intention and outcome.

The question of "means-to-ends" has long been debated in light of the notion of responsibility. In legal terms, an agent can be considered responsible if the crime has not only been intended but also committed through an action that is causally related to a prior intention. Responsibility becomes difficult to determine in situations where, precisely, the causality between one's intention and one's action is *deviant* (Chisholm, 1966; Peacocke, 1979; Knobe, 2006). This problem is well illustrated by the following thought experiment, which highlights the traditional notion of "success through ability" and its mirror, "success through chance" (see Greco, 2009):

Imagine that you are participating in an archery tournament. The target stands at a very long distance. Everybody knows that you're not a very good archer, and *you* know that there is little chance that you will reach the target. Suddenly someone sneezes next to you. The sound makes you startle, and you release the arrow by surprise—and hit the bull's-eye. It was *precisely* your intention, but you feel somehow embarrassed: are you responsible for this success?

In this situation, most people feel uncomfortable in crediting the archer with the achievement. And the archer, although she can pretend that she did hit the target on purpose, knows (or at least feels) that she cannot take full credit for her success. In the present situation, the archer, precisely, doesn't feel responsible, or doesn't feel in control, *even though IM criteria are met*—that is, despite her intention (doing as well as possible) actually matching the resulting, observed outcomes (hitting the bull's-eye). If agency is based on noticing perceptual intention-outcome conjunctions, then one should somehow fail to explain why the archer doesn't take credit for her accidental success. What prevents her from being deluded?

The most obvious answer is that the action specification process has been aborted early. We suggested that this process is meant to causally relate the two terms of the intention-action link. Thus the archer does not feel in control, not because of a perceived mismatch between intention and effects (as the IM account would predict it) but precisely because her intention has been achieved by an action that was not selected or wanted, that is, by an action that had no causal link with the intention to achieve the corresponding effect.

Importantly, the thought experiment of the archer shows that the sense of controlling one's own action is sensitive to the *means* specification process itself. This following distinction is worth stressing: sense of agency is not only sensitive to *whether* actions achieve intention (IM account) but also sensitive to particular actions *by which* an intention is achieved, and thus to processes arising *before* the initiation of the action (premotor account). Agency, and thus responsibility, require reference to means.

The process specifying means-to-ends, by causally relating intentions to actions, is a key component of what makes our actions intentional. In that sense, the IM account fails to explain why the archer's success is *not* intentional—why the archer is *not* responsible for her success. And it fails because it downplays the role of intermediate means in achieving intentional, goal-directed actions. As previously stated, this is a consequence of the ideomotor theory's limited scope: the IM theory describes actions that are under the immediate control of ideation. An action is not considered, among alternatives, as the best way of accomplishing an intended effect; it is *directly* prompted by the mere idea of it.

In an IM view, an intentional action is thus completely driven by the anticipated mental representation of the sequence end state (i.e., by the image of the to-be-produced effect). Accordingly, the archer should take credit for her success, and her action should be considered as intentional: the idea of the target indeed caused the effect to occur, irrespective of how the effect was achieved. Why she actually does not is because an end state is not a goal *by definition*. Indeed, an end state cannot be recognized as a goal unless it is achieved through means that are consistently related to an agent's previous intentions (Pacherie, 2008; Pacherie & Dokic, 2006).

Similarly, an action cannot be recognized as intentional because it achieves an intended end state only. This is the very reason why the archer does not take credit for the achievement: achieving a particular end state *through chance*, rather than through a *desired* action, doesn't make you feel in control. By downplaying the role of means in goal achievement, the IM theory precisely misses how action means, by causally linking intention and perceived effects, contribute to experiencing effects *as intentionally induced*. And the theory misses an important component of what authorship is, namely, the feeling that we are intentionally making things happen by our own actions.

In what follows, we present experimental evidence that, when errors or approximations occur during the action or *means* selection process, the individual's sense of control significantly decreases, over and above any

anticipation of the effect of the selected action. In the example of the archer, this error is consciously available to the subject and consequently affects her experience of action. But clear awareness of error is not necessarily required: a *feeling* that something went wrong during the process may be sufficient to modulate later judgments of control, even without being able to identify or explicitly report the error (see Metcalfe & Greene, 2007).[4]

Action Selection and Sense of Control

A number of studies have shown that sense of control (or "sense of agency") depends on how predictable the consequences of one's action are, getting stronger as the match between intended/predicted and actual outcome of an action gets closer (see Sato, 2009). Accordingly, sense of agency arises when external events that follow our action are consistent with predictions of action outcomes made by the motor system while we perform (Wolpert & Miall, 1996) or simply intend to perform an action (Wegner et al., 2004). According to this view, agency is inferred offline after an action has been performed and its consequences are known. In contrast, little is known about whether and how internal processes involved in the selection of actions may influence subjective sense of control, irrespective of effect predictability.

Recently, Wenke, Fleming, and Haggard (2010) showed that participants' agency could be manipulated through biasing action selection using a subliminal priming procedure. The procedure allowed the researchers to vary sense of control just by inducing a break in the flow from intention to action while holding equal the predictability of action effects.

In the task, participants were instructed to press left or right keys in response to left- or right-pointing arrow targets. Before the target, subliminal left or right arrow primes were presented, unbeknownst to the subject. Prime arrow directions were either identical (compatible condition) or opposite (incompatible condition) to the subsequent target (fig. 14.3). The keypress response to the target caused display of a colored patch as an action effect after a jittered delay. The specific color shown depended on whether the participant's action was compatible or incompatible with the preceding subliminal prime, and not on the prime identity or the chosen action alternative alone. Unlike previous studies, therefore, the primes did not predict the to-be-expected action effects, nor could any specific color be predicted on the basis of the action chosen. Participants rated how much control they experienced over the different colors at the end of each block.

Replicating previous works (Fleming, Mars, Gladwin & Haggard, 2009; Nachev, Rees, Parton, Kennard & Husain, 2005), Wenke and colleagues found that compatible primes facilitated responding, whereas incompati-

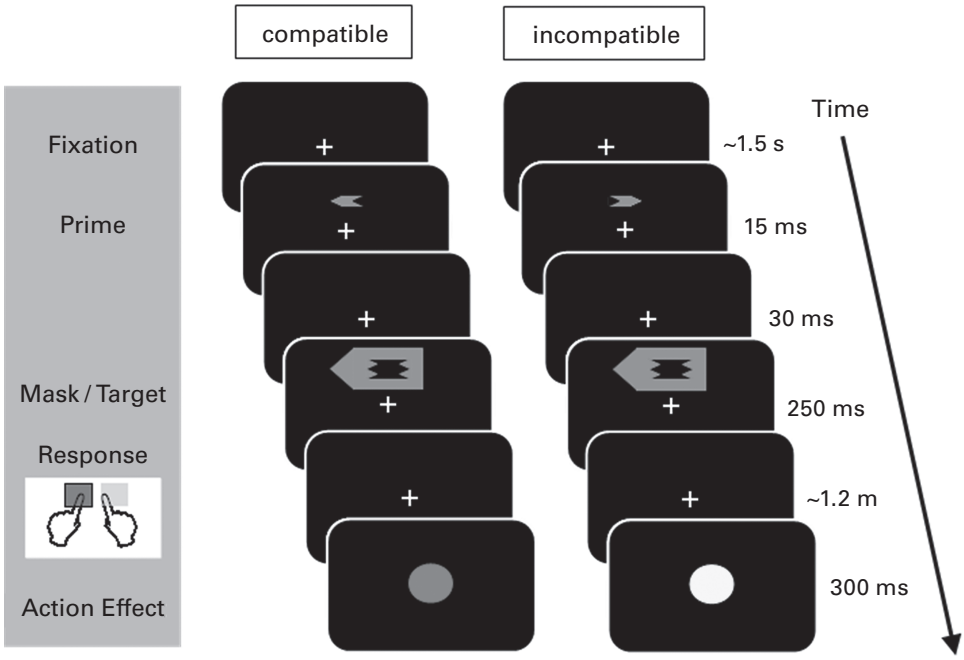

Figure 14.3
Schematic of trial procedure and stimuli (cued-choice conditions only). Example trials from the two possible combinations of the prime-action compatibility (compatible, *left panel*; incompatible, *right panel*). The appearance of the effect was randomly jittered 150, 300, or 450 ms after the keypress to avoid ceiling effects in perceived control. Adapted from Wenke, Fleming & Haggard (2010).

ble primes interfered with response selection. Crucially, priming also modulated the sense of control over action effects: participants experienced more control over colors produced by actions that were compatible with the preceding prime than over colors associated with prime-incompatible actions. Primes supporting the correct or intended response thus facilitated action-selection processes, presumably by differentiating between action alternatives, which rendered the selection process more *fluent*. The key finding of Wenke et al.'s study (2010) is that this fluency produced a heightened sense of control, suggesting that action experience is linked to processes of action selection—being strongest when selection is fluent and uncontested.

Two points are worth emphasizing in Wenke et al.'s study. First, stronger sense of control in fluent action selection was induced although the action

outcomes were equally (un)predictable. Indeed, primes were not designed to predict the effects of action as in previous studies (e.g., Aarts et al., 2005; Linser & Goschke, 2007; Sato, 2009; Wegner & Wheatley, 1999). Therefore participants could not retrospectively base their control judgments on matches between primes and effects alone. Rather, this stronger experience of control could only be explained by the fluency of action selection—that is, by a signal being experienced *before* the action was made and the effect was displayed.

Second, participants were not aware of the conflicting influences of their action. Therefore participants' sense of control could not be based on (conscious) beliefs about how primes might influence action selection. Instead action priming itself presumably directly influenced the subjective sense of control. This supports a recent proposal by Pacherie (2008; see also Synofzik, Vosgerau & Newen, 2008) that sensorimotor conflict, rather than being necessarily conscious (Morsella et al., 2009), elicits the feeling "that something is wrong," without (necessarily) leading to knowledge about *what* is wrong.

These findings suggest that neural activity in action preparation circuits may *prospectively* inform agency, independent of the predictability of the outcome (fig. 14.4). Such a prospective contribution to sense of control

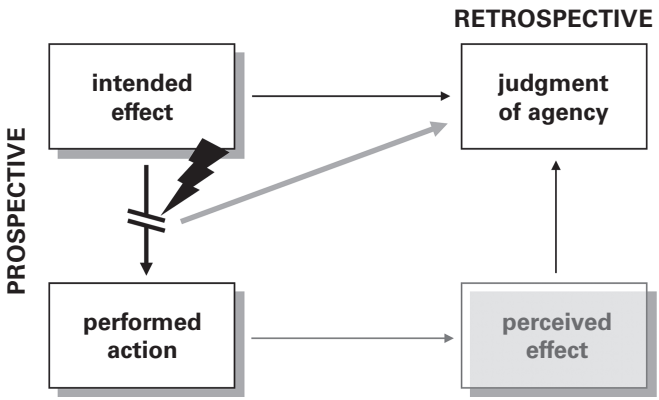

Figure 14.4
Premotor account of action experience. Action selection is conceived as a transformation between intended effects and performed actions. Judgments of control depend on (a) similarity between intended and actual effects inferred retrospectively (thin black arrows), and also on (b) fluency of action selection experienced prospectively (thicker gray arrow). When action selection is perturbed by external influences (broken line), the prospective contribution to the sense of control is reduced.

could be supported by a neural mechanism tracking dysfluency in action selection networks (see Nahab et al., 2011; Miele, Wager, Mitchell & Metcalfe, 2011). By monitoring possible mismatches occurring along the intention-action link, this mechanism would inform us whether our actions are causally linked to our intentions and, in case of a causal discrepancy, would decrease participants' sense of agency over effects of the selected action.

Finally, this finding might suggest an important qualification of recent post hoc determinist views of action control (Wegner, 2002). In its strongest form, this view suggests that human behavior is unconsciously determined by subtle changes in the stimulus environment. Individuals are therefore not even aware of how their behavior is shaped and transformed, although they can retrospectively integrate general information about past actions and environmental cues to make inferences and narrative explanations about their own behavior (Moore, Lagnado, Deal & Haggard, 2009). While participants in Wenke's experiment did not have any conscious experience of the subliminal primes, they did have a real-time *subjective experience* of their own action generation, which reflected the primes' capacity to influence action selection. In this respect, the ability to monitor fluency signals generated *during* action selection might be an important marker for the experience of agency.

Conclusion

We saw that the IM theory downplays the role of intermediate mechanisms in the intention-action link. The reason for this downplaying is twofold. First, the causation between idea and action is direct, and as a consequence, intermediate stages of action selection are irrelevant. Second, one cannot consciously experience the workings of motor programs responsible for enacting actions, as these workings reside beneath consciousness. In an IM view, sense of agency is thus merely retrospective: it is a pure narration constructed in a post hoc manner—from noticing constant conjunctions between prior intentions and observed outcomes.

Contemporary advances in motor neurophysiology contributed to refine the IM account of agency. We saw that this contribution essentially consisted in introducing a biologically plausible model (the predictive forward model) that can be used to track discrepancies occurring along the action-effect chain. Both IM and predictive accounts are important, as they contribute to illuminating two key components of action experience. Judgments of agency require (1) a precise intentional content

(we indeed need to know what we intend to do), and (2) an effect that follows, or resembles, this content. Crucially, we would add a third component: agency requires information about the operation of intermediate mechanisms that select proper means to achieve desired effects. The action/means specification mechanism causally relates intentions to subsequent actions. In this chapter, we argued that causal relation along the intention-action chain is an important part of what makes our action intentional, and thus is a key component of sense of agency—defined as the feeling that we are intentionally making things happen by our own actions.

Notes

1. The ideomotor compatibility effect is another illustration of this direct causation of action by an anticipatory image of the to-be-produced effect. Presentation of a stimulus that resembles the sensory feedback an action may cause activates the action itself. For example, observing hand action (e.g., lifting or tapping gesture) facilitates the corresponding action in participants (Brass, Bekkering, Wohlschlager & Prinz, 2000; Brass, Bekkering & Prinz, 2001).

2. In *A Treatise of Human Nature*, Hume writes: "We may define a CAUSE to be 'An object precedent and contiguous to another, and where all the objects resembling the former are plac'd in like relations of precedency and contiguity to those objects, that resemble the latter'" (1740/1978, p. 170).

3. Attention to these differences has led a number of philosophers to develop dual-intention theories of action (see Pacherie, 2000, for a review). For instance, Searle (1983) distinguishes between prior intentions and intentions-in-action, Bratman (1987) between future-directed and present-directed intentions, Brand (1984) between prospective and immediate intentions, and Mele (1992) between distal and proximal intentions.

4. Imagine, for example, that I intend to turn the light on in a dark room. If, after I push a switch, the light turns on, I will *normally* experience being in control of my action. But what if a presence detector was the real cause of the light turning on? I could still not be fooled precisely because I somehow feel that I have not pressed the switch hard enough—that is, I feel that I have not selected the right force parameters to effectively activate the switch. But I don't need to be consciously aware of why I do not feel in control of the resulting outcome; I just need to *experience* that, when I select the force parameters of my action, something has gone wrong. The term "epistemic feeling" has been coined to describe this subjective, online experience of an error (see Munoz, 2010, for review). In the foregoing example, this feeling is the experiential output of an effort-related cost assessment (see Botvinick, 2007). The error signal resulting from this assessment *at the time of*

action selection may be enough to prevent me from being deluded by purely coincidental action-outcome conjunctions.

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15 Grounding the Human Conceptual System in Perception, Action, and Internal States

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Grounded Cognition

Cognitive scientists classically view cognition as a modular system, separate from other modular systems for perception, action, and internal states. From this perspective, cognitive scientists can safely study cognition as an independent module, focusing on classic cognitive mechanisms associated with attention, working memory, long-term memory, knowledge, language, and thought. Motivated by theoretical arguments across disciplines (e.g., Barsalou, 1999, 2010; Kiefer & Pulvermüller, 2012; Lakoff & Johnson, 1980; Searle, 1980) and by rapidly accumulating empirical results (e.g., Barsalou, 2008a), cognitive scientists increasingly believe, however, that cognition is not modular but instead grounded in four ways.

First, cognition is grounded in modality-specific systems, including those for vision, audition, and taste (e.g., Martin, 2007; Gainotti, 2006; Kiefer, Sim, Herrnberger, Grothe & Hoenig, 2008). For example, when people represent the taste of a pictured food, they represent it as a simulation in the gustatory system (Simmons, Martin & Barsalou, 2005), and when they represent the color of an object, they represent it as a simulation in color regions of the visual system (Simmons et al., 2007). As the rapid accumulation of such experiments demonstrates, cognition relies on representational systems in the modalities.

Second, cognition is grounded in the body and action (e.g., Pulvermüller, 2005). When people represent actions associated with an object, they represent them with simulations in the motor system (Chao & Martin, 2000; Kiefer, Sim, Liebich, Hauk & Tanaka, 2007; Tucker & Ellis, 2004). In social psychology, researchers have further demonstrated that bodily states, such as facial expressions and postures, causally affect cognition, and that cognition in turn affects bodily states (e.g., Barsalou, Niedenthal, Barbey & Ruppert, 2003). Again, the rapid accumulation of such findings demonstrates

that cognition relies on the body and motor system for representational purposes.

Third, cognition is grounded in the physical environment. Since Gibson (1979), researchers have argued that the environment and perceptual mechanisms are both essential for achieving perception, and omitting the environment leads to vacuous theories incapable of explaining perception. More recently, researchers in situated cognition have argued that the cognitive system is organized to support goal-directed action in the environment, such that taking the current physical situation into account is central for understanding the corresponding organization of the cognitive system (e.g., Robbins & Aydede, 2008).

Fourth, cognition is grounded in the social environment. From an evolutionary perspective, humans evolved under strong social pressures, such that the cognitive mechanisms unique to humans are intrinsically social (e.g., Seed & Tomasello, 2010). Central social mechanisms in humans include language (e.g., Donald, 1993), mirroring (e.g., Decety & Grèzes, 2006; Rizzolatti & Craighero, 2004), and perspective taking (Kessler & Thomson, 2010; Tomasello, Kruger & Ratner, 1993). From a grounded perspective, understanding the nature of these critical mechanisms requires grounding them in the social systems in which they function.

Because cognition depends critically on the sensory modalities, the action system, the physical environment, and the social environment, grounded approaches argue that cognition emerges from all these domains (e.g., McClelland, 2010). As a result, cognitive scientists increasingly view cognition as a set of complex emergent phenomena rather than a set of isolated mechanisms in a cognitive module.

Often the term "embodied cognition" is used when referring to this emerging area of research. Although the body does ground cognition, so do the modalities, the physical environment, and the social environment. Thus "embodied cognition" is overly narrow and conveys the inaccurate assumptions that the body dominates cognition and that cognition always depends on the body. More suitably, "grounded cognition" recognizes all forms of cognitive grounding.

In this chapter, we focus on the conceptual system, which contains categorically organized knowledge about the world. In the next three sections, we address theoretical issues associated with grounding concepts. In the final sections, we address six specific hypotheses that follow from this perspective, and review supporting evidence for them, along with methods used to assess grounding.

The Human Conceptual System

As stated in the general definition of the conceptual system in the previous section, knowledge about the world is categorically organized. To appreciate the importance of categorical organization, consider the memory of a digital camera. Because the camera memory does not contain conceptual knowledge about categories, it can only represent holistic bitmapped images of single events and cannot identify components of them as instances of particular categories. In contrast, humans (and other animals) have a powerful attentional mechanism that can focus on various components of experience, including objects, settings, events, mental states, properties, and relations, and then establish bodies of categorically organized knowledge about these components in memory, typically referred to as "concepts." By focusing on the same component of experience repeatedly and integrating memories of it (e.g., dogs), a conceptual representation of the category develops. Over development, tens of thousands of such concepts develop to represent common categories of experience.

Once this system of categorical knowledge is in place, it supports all cognitive activity (e.g., Barsalou 1999, 2003b). During "online" interactions with the environment, the conceptual system plays central roles in high-level perception, such as completing the perception of occluded objects and producing anticipation inferences about how objects will behave. It also enables categorizing what is present and drawing rich inferences that go beyond what is being experienced to provide expertise while interacting with category instances (e.g., how to use a tool). In humans, the conceptual system is also central to "offline" cognition, when people represent situations that are not present in memory, language, and thought.

Semantic memory theories. Given the centrality of the conceptual system in cognition, many theories of it have been proposed. Since the cognitive revolution, the dominant theory is typically referred to as *semantic memory* (e.g., Collins & Loftus, 1975; Tulving, 1972). For our purposes, two central assumptions of this approach are relevant. First, it assumes that the conceptual system is modular in the sense of being separate from the episodic memory system that stores memories indexed in space and time, and also from modal systems that process perception, action, and internal states. Second, as a result of being modular, the representations that underlie categories are amodal, differing from the representations in modal systems by being abstract language-like symbols linked arbitrarily to what they represent.

More specifically, semantic memory theories assume that as someone experiences a category member (e.g., a specific dog), relevant modalities become active to perceive and interact with it. For example, representations in the visual, auditory, and olfactory systems become active to represent how the dog looks, sounds, and smells. Similarly, as the perceiver interacts with the dog, the motor, proprioceptive, and somatosensory systems execute actions, sense actions, and represent how the dog feels. Most importantly, however, semantic memory theories assume that symbolic descriptions are transduced from these modality-specific representations to encode their important properties. For example, symbolic descriptions of visual properties (e.g., legs), auditory properties (e.g., barks), motor actions (e.g., pat), and somatosensory experiences (e.g., soft) are transduced and integrated into conceptual knowledge about dogs. Again, these symbolic descriptions are typically assumed to be amodal, differing from the original modality-specific representations that produced them by being more abstract, arbitrary, and language-like (Fodor, 1975).

Over time, symbolic descriptions accumulate in an integrated conceptual structure that represents the category, taking a wide variety of forms across theories (e.g., feature lists, prototypes, exemplars, frames). When knowledge is needed, these symbolic structures are retrieved to support conceptual processing. Upon hearing the word "dog," for example, symbolic structures that describe dogs are retrieved to represent the word's meaning. Notably, none of the original modality-specific representations that produced these amodal descriptions are typically assumed to be active or relevant. Instead an amodal description suffices.

Grounded theories of the conceptual system. A very different way of thinking about the conceptual system has existed in philosophy for thousands of years and is being reinvented scientifically in modern theories of grounded cognition (e.g., Barsalou, 1999, 2008a, 2010; De Vega, Glenberg & Graesser, 2008; Kiefer et al., 2008; Kiefer & Spitzer, 2001; Pecher & Zwaan, 2005; Pulvermüller & Fadiga, 2010; Semin & Smith, 2008). From this perspective, the conceptual system is not modular but grounded in the modalities for perception, action, and internal states, thereby giving category representations a modal character.

Again, consider conceptual knowledge about dogs. From the grounded perspective, as the modalities become active to represent visual, auditory, olfactory, and somatosensory information from a perceived dog, and as they generate actions, association areas in the brain capture states of these modal systems for later representational use. Rather than transducing symbolic descriptions of these states into an amodal system, the brain simply

attempts to capture states of the relevant modal systems. Across instances over time, these captured states are integrated using associative mechanisms. On occasions when knowledge is needed, captured states are reinstated to support conceptual processing. Upon hearing the word "dog," for example, association areas reactivate modal representations captured from actual experiences with dogs to represent them.

Common misperceptions of grounded cognition. One misperception is that grounded cognition is necessarily exclusively empiricist. Although concepts certainly reflect experience, they also have strong biological bases that scaffold learning. There is no a priori reason why grounded conceptual structures cannot have a strong genetic basis, especially in the sensorymotor feature and association areas that underlie them. Similarly, some concepts themselves may have a genetic basis in simulation mechanisms (e.g., Hoenig et al., 2011; Kiefer et al., 2007; Simmons & Barsalou, 2003).

Another misperception is that grounded accounts essentially view the conceptual system as a recording system, similar to cameras and other recorders that only capture holistic bitmapped images, thereby being unable to construct symbolic representations. As described later, however, this assumption does not necessarily follow, given that grounded approaches implement symbolic systems (e.g., Barsalou, 1999, 2003a, 2005a).

A final misperception is that all concepts must be grounded in the perception of the external world. Again, however, this assumption does not necessarily follow. There is no reason that internal states cannot be captured and reenacted in the same manner as external states. As internal states for emotion, interoception, and mentalizing occur, attentional and associative mechanisms integrate them into conceptual structures. As described later, captured internal states play central roles in concepts, especially abstract ones.

Themes Associated with Grounded Conceptual Systems

Grounded approaches to the conceptual system typically exhibit four themes: simulation, emergence, dynamic representation, and situatedness.

Simulation. As just described, grounded theories typically assume that captured multimodal states accumulate across instances to establish the concept that represents a category. Grounded theories further assume that small subsets of these captured states can later be reactivated on a given occasion to represent the category in the absence of an instance. Upon hearing the word "dog," captured states for dogs are reactivated to provide likely inferences about the category. Many researchers refer to these reactivations

as *simulations*; namely, the brain is simulating the state it would be in if it were actually experiencing a category instance. Thus simulations are temporary, situation-specific representations constructed dynamically from an established concept in memory to represent a category.

Researchers further assume that simulations take a wide variety of forms (e.g., Barsalou, 1999). On some occasions, simulations might be fully conscious, as in mental imagery. On many others, however, simulations may be partially, mostly, or even completely unconscious while still having significant impact on cognition (e.g., Barsalou et al., 2003; Kiefer et al., 2008). Simulations can vary widely across other dimensions, as well. On some occasions, simulations may be relatively vague and sketchy, only reinstating partial information in original experiences. On other occasions, simulations may be vivid and detailed. Analogously, simulations can reflect the average of many instances or represent a single instance. Finally, simulations may range from being relatively veridical to being highly distorted.

Considerable evidence has accumulated across multiple disciplines for simulation mechanisms, not only in knowledge representation but in all other cognitive processes from perception to social cognition (Barsalou, 2008a). We believe increasingly that simulation is a basic computational process in the brain that takes many diverse forms across myriad cognitive processes. Importantly, however, other computational mechanisms are undoubtedly important as well for processing concepts, especially language (Barsalou, Santos, Simmons & Wilson, 2008; Paivio, 1986).

Emergence. As described earlier, grounded cognition assumes that cognitive phenomena emerge from diverse domains including perception, action, and internal states. Analogously, grounded views propose that concepts emerge from distributed systems. From this perspective, a concept emerges from all the brain areas that process properties of its instances. For example, brain areas that process visual, auditory, olfactory, and somatosensory properties of dogs store conceptual knowledge about them, along with brain areas that process relevant actions and affective responses toward them. Rather than being localized in one neural system, the properties that represent dogs are distributed across relevant neural systems dedicated to perception, action, and internal states, with the concept for dogs emerging from them.

It follows from this account that different kinds of concepts should emerge from different collections of brain areas (e.g., Cree & McRae, 2003). Martin (2007), for example, documents different multimodal profiles for living versus nonliving things. Whereas specific brain areas represent the

visual form and motion of living things, different (but adjacent) brain areas represent the visual form and motion of tools, along with additional areas that represent tool actions (Hoenig, Sim, Bochev, Herrnberger & Kiefer, 2008; Kiefer, 2001, 2005).

Similar findings are accumulating in other conceptual domains. Much research, for example, has documented the distributed circuits that underlie social concepts (e.g., Northoff et al., 2006; Van Overwalle, 2009; Simmons, Reddish, Bellgowan & Martin, 2010). Specifically, social concepts emerge from distributed areas that process mentalizing, emotion, interoception, visual motion, and other properties associated with individuals and the self. Analogously, emotions emerge from the neural systems that process properties relevant for emotion rather than from discrete subcortical modules (e.g., Kober et al., 2008; Wilson-Mendenhall, Barrett, Simmons & Barsalou, 2011). Another intriguing distinction is between concepts about entities and events in the external world versus concepts for internal evaluations of them, with different distributed circuits representing extrinsic versus intrinsic concepts (e.g., Golland, Golland, Bentin & Malach, 2008). In all these cases, concepts emerge from diverse neural systems relevant for processing their properties.

Dynamic representation. Researchers often view a concept as a static data structure in memory that always represents a category in a fixed way (e.g., a definition, prototype, frame). Conversely, grounded cognition often views a concept as a dynamic system capable of producing an infinite number of simulations that each represent relevant information about the category in a specific situation (e.g., Barsalou, Breazeal & Smith, 2007).

Many findings demonstrate that concepts produce temporary, situation-specific representations of categories dynamically (for reviews, see Barsalou, 2008c; Yeh & Barsalou, 2006). In behavioral experiments, much research demonstrates that different information becomes active for the same concept in different situations (e.g., Barsalou, 1987, 1989). In neuroimaging experiments, Hoenig et al. (2008) and Wilson-Mendenhall, Barrett, et al. (2011) found that different neural circuits became active in different situations to represent the same concept.

Situatedness. From the perspective of grounded cognition, the simulations that concepts produce dynamically do not exist in a vacuum. When someone represents the category of hammers, for example, she does not just simulate a hammer floating in space. Instead she situates the simulation, representing it in a setting, along with relevant objects, with agents performing actions that produce events and internal states (as in hammering a nail into a board). Rather than being like a dictionary or encyclopedia,

the conceptual system is more like an instructional manual that guides intelligent, goal-directed action in the current situation (e.g., Barsalou, 2003b; Robbins & Aydede, 2008).

Much research demonstrates the situated character of the dynamic representations that concepts produce (for reviews, see Barsalou, 2008c; Yeh & Barsalou, 2006). In Wu and Barsalou (2009), for example, participants generated properties of object categories (e.g., car). Not surprisingly, many properties described the objects (e.g., wheels). Significantly, however, many properties described background situations, including settings, events, and internal states. Although participants were asked explicitly to describe objects, they situated them implicitly (see also Barsalou & Wiemer-Hastings, 2005; Santos, Chaigneau, Simmons & Barsalou, 2011).

Numerous neuroimaging studies similarly demonstrate the situated character of the dynamic representations that concepts produce. Chao and Martin (2000) presented participants with static pictures of isolated manipulable artifacts with no mention of action or function. Nevertheless a grasping circuit became active, indicating that participants situated the objects with respect to action (for a review, see Lewis, 2006). Simmons et al. (2005) performed an analogous experiment with pictures of food and found that participants situated the foods as if consuming them. Gil-da-Costa et al. (2004) similarly found that monkeys situated monkey calls as if experiencing them in social situations (see also Barsalou, 2005b).

Challenges for Grounded Theories of Concepts

Researchers sometimes propose that grounded theories are best suited for explaining concrete concepts, such as those for objects and simple behaviors, given their reliance on sensory-motor systems. Such proposals further question whether grounded theories can explain so-called abstract concepts and symbolic operations, which appear to rely less on these systems. In this section, we propose that neither concern is warranted and that grounded theories are well suited to explain both abstract concepts and symbolic operations.

Abstract concepts. By definition, abstract concepts do not refer to physical objects that constitute targets of sensory-motor interactions (e.g., *truth*). We question, however, whether abstract concepts are actually abstract, and propose instead that they are grounded in situated experience, similar to concrete concepts. From the grounded perspective, the distinction of concrete versus abstract is a misnomer, given that both kinds of concepts are grounded in situations.

Our account begins by assuming that all concepts are situated (Barsalou, 1999). In general, all concepts are represented in a setting with relevant objects and agents performing actions that produce events and internal states. Where concepts differ, we argue, is in how they focus attention on certain parts of situations, leaving other parts in the background. Whereas so-called concrete concepts focus attention on well-bounded parts of external situations, such as objects, settings, and simple actions, so-called abstract concepts focus attention on internal states and complex events. For each type of concept, representations of entire situations underlie conceptual processing, but with different parts being focal (for a related perspective, see Kiefer & Pulvermüller, 2011).

Barsalou and Wiemer-Hastings (2005) offered preliminary support for this account. When participants generated properties for concrete and abstract concepts (e.g., *bird* vs. *truth*), they produced broad situational information for both, including properties that described settings, objects, events, and internal states. As further predicted, however, concrete concepts focused more on external objects, whereas abstract concepts focused more on settings, events, and internal states. Additionally, abstract concepts contained more organizational structure, suggesting that they play central roles in integrating situational information.

Wilson-Mendenhall, Simmons, Martin, and Barsalou (2011) offered further support for this account. In a neuroimaging experiment, participants represented abstract concepts with simulated internal states. When representing the abstract concept of *convince*, brain areas associated with mental states and social interaction became active. When representing the abstract concept of *arithmetic*, brain areas associated with processing number became active. Additionally, abstract concepts activated more areas than concrete concepts, suggesting again that abstract concepts tend to integrate broad situational information. Abstract concepts also activated more visual areas, calling into question their status as "abstract."

Wilson-Mendenhall, Barrett, et al. (2011) also assessed neural activations for abstract concepts. For the abstract concept of *observe*, the visual and auditory systems became active as if participants were simulating the experience of visual and auditory observation. More generally, all abstract concepts activated different distributed circuits in different situations, further implicating the situated character of conceptual processing.

Symbolic operations. Classic theories assume that cognition is inherently symbolic, where "symbolic" means that cognition operates on conceptual interpretations of experience, not on analog representations of the experiences themselves (e.g., Fodor, 1975; Pylyshyn, 1973). When someone

perceives a forest scene, for example, concepts for trees, flowers, squirrels, et cetera, categorize relevant entities, thereby interpreting them as instances. Conversely, when a camera takes a picture of the scene, it only represents bitmapped images of forest entities together in an undifferentiated holistic manner. Because concepts do not interpret these entities, an explicit symbolic representation of the scene does not exist. We show next that it is nevertheless possible to implement symbolic operations using grounded mechanisms (e.g., Barsalou, 1999, 2003a, 2005a).

As described in the following paragraphs, symbolic theories assume that type-token predication, categorical inference, and conceptual combination are central to cognition. We agree with the central role of these symbolic operations in cognition but disagree with the standard assumptions that amodal symbols implement them.

First consider type-token predication. When an individual is categorized as an instance of a concept, a type-token predication results, specifying that the individual is believed to be an instance of the concept (e.g., categorizing an individual as a *dog* specifies that the individual is believed to be a dog). According to classic theories, an amodal symbolic structure represents this predication, but according to grounded theories, a modal simulation represents it instead.

To test the grounded view, researchers have developed paradigms for assessing whether predicates are grounded in the brain's modal systems. Simmons et al. (2007), for example, asked participants to verify whether color predicates (e.g., yellow) could be accurately predicated of objects (e.g., banana). According to grounded views, participants should simulate yellow and other colors in color-processing regions of the brain when predicating them of objects. Simmons et al. obtained support for this prediction, as have many other researchers who have studied diverse predicates both behaviorally and neurally (for reviews, see Barsalou, 2008b; Hoenig et al., 2008).

Next consider categorical inference, namely, the process of inferring the properties of an individual, once a concept has been predicated of it (e.g., inferring that an individual is likely to bark once the concept *dog* has been predicated of it). Extensive evidence further implicates grounded views in the projection of categorical inferences. In research on situated conceptualization, studies demonstrate that once a concept is predicated of something, a wide variety of grounded inferences follow. In Chao and Martin (2000), for example, predicating a tool category of an object generated motor inferences about interacting with it. Similarly, in Simmons et al. (2005), predicating a food category of an object generated gustatory inferences about eating it. For reviews of many other such findings, both behavioral and neural, see Barsalou (2008a, 2008b, 2008c).

Finally, modest evidence implicates simulation in conceptual combination (the process of combining simple concepts into complex ones). When Wu and Barsalou (2009) asked participants to produce properties true of conceptual combinations (e.g., *rolled-up lawn*), they found that occluded properties were produced less often than unoccluded properties, implicating visual simulations in the combination process. More indirectly, the extensive evidence now implicating modal simulation in text comprehension further suggests that conceptual combination is grounded (e.g., Pecher & Zwaan, 2005; De Vega et al., 2008). Because text comprehension requires extensive combination of concepts at the phrase, sentence, and discourse levels, evidence that modal representations are active during text comprehension potentially implicates them in conceptual combination, although more direct assessments are necessary.

Testing Specific Predictions of Grounded Cognition Theory

In previous sections, we characterized a concept as the representation of a category in memory that emerges from distributed modal systems in the brain for perception, action, and introspection. In turn, simulations are constructed dynamically from the concept that represents the category in a situated manner on specific occasions. From these general assumptions, we derive the following six critical predictions that make it possible to empirically distinguish grounded cognition theory from amodal theories: (i) accessing a concept should activate the modality-specific systems that code the corresponding conceptual features (e.g., visual, auditory, action related); (ii) as conceptual processing is based on a partial reinstatement of activity within sensory-motor systems, conceptual and sensory-motor processing should exhibit similarities at a functional and neuroanatomical level; (iii) the situated and dynamic nature of conceptual representations results in a context-dependent activation of conceptual features in sensory-motor systems; (iv) the activation pattern in sensory-motor systems reflects access to conceptual features that constitute the concept rather than input or output processes such as object perception, imagery, or overt action (cf. Mahon & Caramazza, 2009; McClelland & Rogers, 2003; Rogers et al., 2004); (v) modal representations have a functional significance in conceptual tasks and affect behavioral performance, rather than being a concomitant effect in the sense of an epiphenomenon; (vi) concepts are experience-dependent representations that reflect the individual's past interactions with the physical, social, and internal word.

In the remainder of this chapter, we provide an overview on recent investigations that tested one or more of these predictions of grounded

cognition theory. As the literature in the field is abundant, we focus on selected examples, which test these predictions in a paradigmatic way. Given that they concern cognitive processing at different levels of analysis, we draw on a variety of methodologies and approaches to address them convincingly.

Sensory-Motor Activity during Conceptual Tasks: Neurophysiological Recording Techniques

Neuroimaging studies using positron-emission tomography (PET) or functional magnetic resonance imaging (fMRI), as well as measurements of electrical brain activity with electroencephalogram (EEG) or magnetoencephalogram (MEG), are highly valuable sources of evidence for testing the predictions of grounded cognition theory. These neuroscientific techniques provide direct information for the involvement of modality-specific sensory and motor systems during conceptual tasks and thus considerably constrain theoretical assumptions regarding the structure of conceptual memory (for a similar argument in the context of the imagery debate, see Kosslyn, 1994).

Localizing Brain Activity during Conceptual Processing

Neuroimaging results have provided converging evidence on the differential involvement of modality-specific brain areas in the processing of words and concepts of different kinds (e.g., vision-related concepts versus action-related concepts). In line with grounded cognition theory, PET and fMRI studies in healthy participants (e.g., Hoenig et al., 2008; Martin, Wiggs, Ungerleider & Haxby, 1996; Simmons et al., 2005) demonstrated activation in sensory-motor brain areas in a range of conceptual tasks (for an overview, see Kemmerer & Gonzalez-Castillo, 2010; Kiefer & Pulvermüller, 2012; Martin, 2007; Pulvermüller & Fadiga, 2010).

Convincing evidence suggests that conceptual and perceptual processing functionally and neuroanatomically overlaps in sensory brain regions (Kiefer et al., 2008): visual recognition of words denoting objects, for which acoustic features are highly relevant (e.g., sound-related concepts such as "telephone"), ignited cell assemblies in left posterior superior and middle temporal gyri (pSTG/MTG) that were also activated by sound perception (fig. 15.1A [plate 4]). Importantly, activity within this part of auditory association cortex increased selectively as a function of acoustic, but not of visual and action-related, feature relevance, showing that left pSTG/

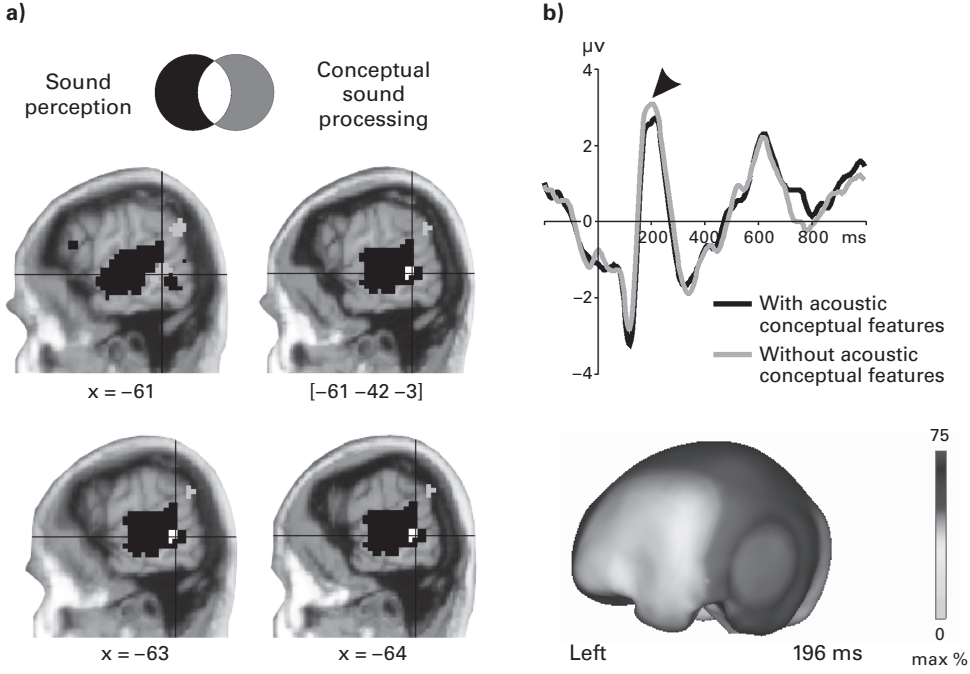

Figure 15.1

The grounding of concepts in auditory brain systems. (a) Functional-anatomical overlap between conceptual and perceptual processing of acoustic features. Increased functional activation to words with acoustic conceptual features (conceptual processing) overlaps with brain activation during listening to real sounds (sound perception) in left posterior superior and middle temporal gyrus (pSTG/MTG). Shown are contiguous slices centered on the peak coordinates. (b) Time course of conceptual processing of acoustic features. *Top*: Event-related scalp potentials to words with versus without acoustic features at central electrodes. Potentials are collapsed across central electrode sites. The arrow indicates the onset of the effect. *Bottom*: Brain electrical sources of scalp ERPs: maps of cortical currents calculated according to the minimum norm algorithm from the ERP difference waves (with versus without acoustic features). Maps are shown for the respective maxima in global field power. Strongest cortical currents (visualized in blue color) were observed in and close to left pSTG/MTG. Adapted from Kiefer et al. (2008). (See plate 4.)

MTG specifically codes acoustic conceptual knowledge (Kiefer et al., 2008). These results demonstrate that access to concepts recruits auditory areas that are also active during auditory perception. Activation of sensory brain regions in conceptual processing has been documented not only for the auditory modality but also for vision (Chao, Haxby & Martin, 1999; Sim & Kiefer, 2005) and even taste (Gonzalez et al., 2006; Simmons et al., 2005). This shows that the modal representation of conceptual features in the corresponding sensory brain areas is a general principle that applies to many sensory modalities.

Other work has investigated the significance of the motor system for conceptual processing (for reviews, see Gallese & Lakoff, 2005; Pulvermüller, 2005; Pulvermüller & Fadiga, 2010). Conceptual processing of action words activates motor areas as a function of the body part involved in carrying out the action (Hauk, Johnsrude & Pulvermüller, 2004). The activations for arm- and leg-action concepts partially overlapped with the activity pattern evoked by real body movements, that is, when the finger and foot, respectively, were moved by the participants.

These examples impressively confirm the first two predictions of grounded cognition theory: conceptual processing engages sensory-motor systems, which represent the corresponding conceptual features in a modal fashion (e.g., visual, auditory, gustatory, olfactory, or action-related features); and furthermore, activity in sensory-motor areas during conceptual processing partially overlaps with activity typically involved in perception and action. These results are difficult to reconcile with amodal approaches to conceptual memory, which assume that concepts are processed in heteromodal association cortex distinct from perception and action (Mahon & Caramazza, 2009; Rogers et al., 2004; Tyler & Moss, 2001). Heteromodal association cortex receives input from lower-level modality-specific brain areas and integrates information in an amodal fashion. Neuroimaging work (Hoenig et al., 2008) further demonstrates that the activity pattern in sensory-motor regions in response to a given concept strongly varies with the task, suggesting a situation-dependent recruitment of modal conceptual features (Barsalou, 1982; Kiefer, 2005). This finding supports the notion of situated, dynamic concepts, as stated in our third prediction.

Time Course of Brain Activity during Conceptual Processing

Neuroimaging studies using fMRI or PET demonstrate that sensory-motor cortex is activated during conceptual tasks. They do not inform us, however, whether activity in modality-specific cortex reflects access to conceptual features that constitute the concept as proposed by the grounded cognition

theory. According to this view, modal conceptual features can be activated unconsciously and rapidly, thereby preceding relatively slow and conscious imagery processes. Alternatively, it is conceivable that the concept proper is stored in an amodal format in heteromodal association cortex, whereas activity in modality-specific cortex indexes slow postconceptual processes such as imagery or associative elaboration (Mahon & Caramazza, 2009; McClelland & Rogers, 2003; Rogers et al., 2004). These two alternative explanations make different predictions regarding the time course of brain activity in sensory-motor areas during conceptual tasks. According to grounded cognition theory, activation in sensory-motor areas should emerge at early processing stages concurrent with the word or object recognition process, which is estimated to be completed between 150 and 200 ms (Kiefer et al., 2008). According to the imagery interpretation, sensory-motor activity should occur only after the access to the (amodal) concept in later intervals between 300 and 500 ms. Although grounded cognition theory does not preclude a late access to modal conceptual features, it is difficult to differentiate between conceptual processing and imagery if sensory-motor activation is observed in time windows later than 300 ms (Kiefer, 2005; Sim & Kiefer, 2005).

Due to their high temporal resolution, EEG or MEG recordings are highly suitable to track the time course of sensory-motor activity during conceptual tasks. In support of grounded cognition theory, several studies, which used even-related potentials (ERPs) of the EEG in addition to fMRI scanning, found evidence for early activity in sensory-motor systems in conceptual tasks (for the fMRI results, see the previous section). Sound-related concepts (see fig. 15.1B) activated auditory association cortex starting at 150 ms after word onset (Kiefer et al., 2008). Action-related concepts ignited motor areas within 200 ms after the critical meaningful stimulus could be recognized (Pulvermüller, 2005). Some studies even found activity in modality-specific cortex at about 100 ms after stimulus onset (Hoenig et al., 2008; Kiefer, Sim, Helbig & Graf, 2011). These results clearly confirm our fourth prediction, which states that sensory-motor activity reflects access to conceptual features rather than exclusively late postconceptual processes.

Causal Influence of Sensory-Motor Representations on Performance in Conceptual Tasks

Although several lines of evidence indicate that conceptual representations are grounded in sensory-motor systems, neuroimaging and electrophysiological studies only provide correlational information regarding

the involvement of modality-specific brain circuits in conceptual processing. They cannot answer the question of whether sensory or motor representations are necessary for conceptual processing and thus play a causal role. Addressing this question is theoretically highly important because the involvement of modality-specific brain regions in conceptual tasks may only be auxiliary or concomitant, while conceptual information proper is represented in an amodal fashion (Mahon & Caramazza, 2009) in heteromodal association cortex, possibly close to the temporal pole (McClelland & Rogers, 2003; Rogers et al., 2004).

In the following sections, we give an overview on studies that provide theoretically informed empirical demonstrations for a causal role of modal representations in conceptual tasks. They confirm our fifth prediction, highlighting the functional role of sensory-motor representations in conceptual tasks, and rule out the possibility that modal representations are only auxiliary or concomitant.

Behavioral Priming and Interference Paradigms

Behavioral experiments using priming (facilitation of a target response due to a previous stimulation) or interference (impairment of a target response due to a previous stimulation) paradigms tested the functional role of sensory-motor representations (for a review, see Barsalou, 2008a). A previous activation of sensory (Vermeulen, Corneille & Niedenthal, 2008) or action-related representations (Helbig, Graf & Kiefer, 2006; Kiefer et al., 2011) is shown to modulate subsequent performance in conceptual tasks, in particular when the corresponding sensory or motor information is highly relevant to the target concept (Witt, Kemmerer, Linkenauger & Culham, 2010). Because sensory-motor stimulation influences performance in a conceptual task, we can conclude that conceptual processing is causally linked to modal representations. For instance, observing an action movie as a prime (e.g., seeing a hand hammering) facilitates conceptual access to a subsequently presented manipulable target object when the target is associated with a similar action as the prime movie (e.g., ax) compared with a dissimilar one (e.g., saw) (Helbig, Steinwender, Graf & Kiefer, 2010). Action-priming effects have also been obtained for prime objects, which afforded a similar action as the target objects (Helbig et al., 2006; Kiefer et al., 2011). Behavioral experiments with interference paradigms have found that a visual interference task specifically slows visual property verifications, whereas an auditory interference task specifically slows auditory property verifications (Vermeulen et al., 2008). These findings from

priming and interference paradigms demonstrate that sensory-motor representations play a functional role in conceptual processing.

Transcranial Magnetic Stimulation and the Effect of Brain Damage

The causal role of sensory-motor representations for conceptual processing can also be tested at a neural level. Transcranial magnetic stimulation (TMS) can be used to temporarily influence the functional state of small areas in modality-specific cortex. TMS can improve or hurt performance as a function of the stimulation protocol: low-frequency stimulation (< 1 Hz) typically induces neural inhibition and as a consequence inferior performance, whereas stimulation with higher frequencies (> 1 Hz) induces neural excitation leading to superior performance (e.g., faster reactions). TMS to the motor cortex (Buccino et al., 2005; Pulvermüller, Hauk, Nikulin & Ilmoniemi, 2005) and to the parietal visuomotor system (Pobric, Jefferies & Lambon Ralph, 2010) influences performance in conceptual tasks specifically for stimuli (e.g., action words, manipulable objects), for which action-related information is highly relevant. Crucially, magnetic stimulation of the hand area in motor cortex improved the recognition of arm-related words, whereas TMS to the foot region improved leg word processing (Pulvermüller et al., 2005). Stimulation of the motor system therefore has an effect on the processing of action-related concepts in an effector-specific fashion, as suggested by neuroimaging (Hauk et al., 2004).

The causal role of modality-specific cortex can also be tested by neuropsychological studies in brain-damaged patients with focal lesions to sensory or motor cortex, although lesions may sometimes be widespread or damage neural connections, thereby limiting the interpretation of the findings. Nevertheless results converge on the pattern that lesions in frontal and parietal motor areas selectively impair conceptual processing of action verbs (Vigliocco, Vinson, Druks, Barber & Cappa, 2011) and manipulable objects (Gainotti, 2006) while leaving comprehension of visually defined nouns intact (Neininger & Pulvermüller, 2003). In contrast, right temporo-occipital lesions produce an impairment for visually defined nouns (Neininger & Pulvermüller, 2003). Similarly, damage to modality-specific auditory cortex selectively impairs processing of sound-related concepts (Trumpp, Kliese, Hoenig, Haarmaier & Kiefer, 2012). TMS and neuropsychological studies thus demonstrate that modality-specific cortex is necessary for conceptual processing: temporal interference with TMS or permanent damage in modality-specific cortex in patients affects access to concepts, for which the corresponding sensory-motor information is highly relevant.

Experience-Dependent Plasticity of Conceptual Representations in Sensory-Motor Systems

In line with the sixth prediction of grounded cognition theory, we describe convincing demonstrations that concepts are represented in sensory-motor areas through the learning-based formation of cortical cell assemblies. Training studies investigated the experience-dependent acquisition of conceptual representations for novel objects (James & Gauthier, 2003; Kiefer et al., 2007; Weisberg, van Turennout & Martin, 2007). For instance, the formation of sensory-motor representations establishing a concept was investigated by training human participants with novel objects ("nobjects") under different training conditions (Kiefer et al., 2007). During training (fig. 15.2A [plate 5]), participants were asked to either make an action pantomime toward a detail feature of the novel object, which signaled a specific object function, or to point to it. In a categorization task at test, the neural correlates of the acquired conceptual representations were assessed by measuring electrical brain activity (fig. 15.2B[plate 5]). Only in the pantomime group, in which a meaningful action was performed toward the object during training, early activation in frontal motor regions and later activation in occipito-parietal visual-motor regions were found, indicating that action representations essentially constitute the concept. In the pointing training group, in which the action during training was not meaningfully related to the object, these effects were absent, suggesting that concepts were not grounded in action.

Experience-dependent plasticity of conceptual representations can be demonstrated not only with novel but also with real objects or events. Professional musicians, but not musical laypersons, activate auditory association cortex when accessing conceptual knowledge about musical instruments (Hoenig et al., 2011). Similarly, hockey players as well as hockey fans showed more activity in dorsal premotor cortex than novices when they passively listened to sentences describing ice hockey actions (Beilock, Lyons, Mattarella-Micke, Nusbaum & Small, 2008).

Conclusion

Grounded cognition theory assumes that conceptual cognition is essentially grounded in perception, action, and internal states. Accordingly, concepts become established by the corresponding modal systems that typically process instances of the respective categories in interaction with the physical and social world. Our view of concepts contrasts strongly with

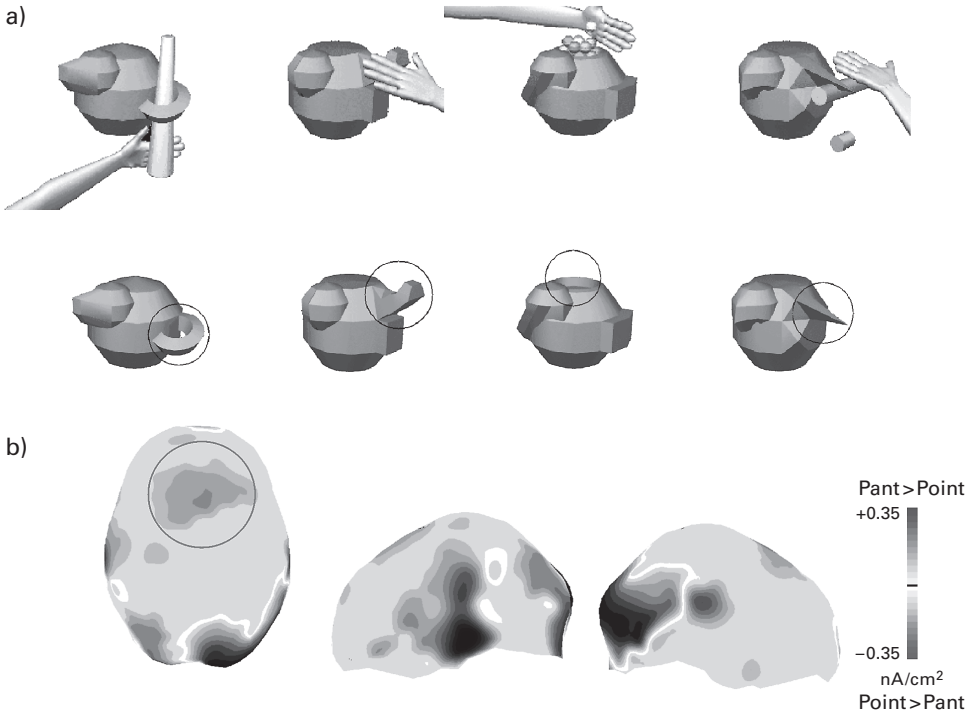

Figure 15.2
Experience-dependent plasticity of conceptual representations in the visuomotor system. (a) Examples of the novel 3-D objects ("nobjects"), for which conceptual knowledge was acquired during training and demonstrations of the different training conditions. *Top*: Actions associated with the detail feature in the pantomime training group. *Bottom*: Pictures highlighting the detail feature to be pointed to in the pointing training group. (b) Minimum norm source estimates obtained from grand-mean scalp ERPs at test after the training during a categorization task. Shown are difference maps between the pantomime and the pointing condition at 117 ms after picture onset. Note the fronto-central activation (yellow circle) close to the premotor cortex in the pantomime group. Adapted from Kiefer et al. (2007). (See plate 5.)

classical theories that view concepts as amodal mental entities in which original modal information is transformed into a common abstract representation format.

At a theoretical level, we have shown that grounded cognition can in principle explain many relevant phenomena in conceptual cognition, including predication, inferences, and abstract concepts. This theoretical analysis shows that grounded cognition has explanatory power comparable to classic amodal theories. From basic assumptions of grounded cognition, we derived six critical predictions that serve to distinguish our modal theoretical stance from amodal theories. We described methodologies that are well suited to test these predictions, and presented findings from the literature that confirm our assumptions. As empirical tests of grounded cognition require the analysis of both structure and processes within the conceptual system, a multimethod approach to conceptual cognition is necessary, including behavioral studies and neurophysiological recording techniques, as well as neuropsychological lesion and TMS studies. The results reviewed here confirm grounded cognition at several levels of analyses. Conceptual processing involves the systems for perception, action, and internal states at a neural and functional level in a predictable fashion. Modal representations that underlie perception and action are accessed rapidly in conceptual tasks, demonstrating that modality-specific processes reflect access to conceptual features rather than postconceptual associative or imagery processes. Finally, and most importantly, processes in modality-specific systems depend on previous sensory-motor experience and are causally linked to performance in conceptual tasks.

Although much progress has been made in collecting critical evidence to support grounded cognition, research on some topics is just beginning. We want to highlight three areas in which further empirical work is needed. First, in contrast to findings demonstrating the involvement of sensory-motor systems in conceptual tasks at a correlational level, more evidence regarding the causal role of the modality-specific systems for performance in conceptual tasks would further strengthen grounded cognition theory. Second, although several lines of evidence demonstrate the importance of sensory-motor systems for conceptual processing, this does not preclude the possibility of an additional supramodal conceptual system. For instance, a hybrid theory suggests a central hub neuroanatomically located in the anterior temporal lobe that facilitates the integration of the distributed sensory-motor representations into a coherent concept (Patterson, Nestor & Rogers, 2007; for a detailed discussion, see Kiefer & Pulvermüller, 2012). Finally, there is little empirical work on the grounding of abstract concepts

in perception, action, and internal states. In particular, clarifying the nature of abstract concepts will decide whether grounded cognition theory will qualify as a general framework for conceptual cognition.

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16 Volition in Action: Intentions, Control Dilemmas, and the Dynamic Regulation of Cognitive Control

Thomas Goschke

Introduction

After having been a topic of philosophical debate for millennia, in the past two decades volition, voluntary action, and cognitive control have become the focus of intense research efforts in experimental psychology and cognitive neuroscience. While the term *volition* is often associated with the idea of a "free will" exempt from causal determination,[1] this research approaches volition from a naturalistic stance that aims to elucidate the cognitive and neural mechanisms mediating voluntary action. From this perspective, the concept of volition is a summary term that denotes a set of specific cognitive mechanisms, which enable humans to *anticipate* future consequences of actions, to flexibly *reconfigure* response dispositions, and to *inhibit* habitual or impulsive responses in favor of long-term goals. The evolution of these control capacities has decoupled action from the immediate stimulus situation and current need state and is the basis for the remarkable flexibility of voluntary action. Accordingly, what distinguishes a voluntary action (e.g., intentionally kicking one's leg) from a knee-jerk reflex is not that the voluntary action is undetermined but that it is *determined in special ways* (Dennett, 2003; Goschke, 2003; Roskies, 2010). The critical question is thus not whether but *how* voluntary action is determined.

In this chapter I address three aspects of this question. After a brief exposition of cognitive foundations of voluntary action in the first section, in the second I examine the role of intentions in the causation of action. Contrary to the intuitive impression that intentions are immediate "triggering" causes of actions, I argue that intentions play a much more indirect role and can be conceived of in terms of internal *constraints* that "preconfigure" response dispositions and thereby bias which responses are subsequently activated by stimuli. This view of intentions will shed new light on recent claims that conscious will is an illusion and on the interplay of

conscious and unconscious determinants of action. In the third section, I examine cognitive and neural mechanisms of volitional control processes that support the realization of intentions despite competing habitual or emotional responses. In the fourth, I address the central yet neglected question of how cognitive control processes are themselves regulated. I outline a theoretical framework according to which voluntary action in a changing environment confronts agents with a set of *control dilemmas*, which afford a dynamic balance between antagonistic control demands. Within this framework, I discuss recent evidence on how complementary control processes are modulated by emotions and neuromodulatory systems.

Cognitive Foundations of Voluntary Action

A central feature of voluntary actions is that they are not fully determined by the immediate stimulus situation but depend on mental representations of intended goals and anticipated effects. As was stressed by nineteenth-century scholars such as Lotze (1852) and James (1890), what makes a movement a voluntary action is that it involves an "anticipation of the movement's sensible effects, resident or remote" (James, 1890, Vol. 2, p. 521). During ontogenesis, we learn to predict with increasing accuracy which effects actions have in a given context and thereby become able to select actions that produce desired effects, that is, serve to attain goals (Elsner & Hommel, 2001; Shin, Proctor & Capaldi, 2010). Goals usually refer to *distal* sensory effects of actions and can differ widely in their abstractness, temporal distance, and hierarchical structure (Hommel, Müsseler, Aschersleben & Prinz, 2001).

While the capacity to associate behaviors with their effects—which we share with many animals, as demonstrated by a century of research on instrumental learning—constitutes a minimal condition for voluntary action, human voluntary action rests on a much richer set of evolved anticipatory and cognitive control capacities.

Episodic Future Thinking and Anticipation of Future Needs

Whereas the simplest instances of voluntary action involve anticipations of immediate sensory effects (e.g., that flipping a switch turns on the light), we are able to form expectations about consequences of actions that are arbitrarily remote in time and space (e.g., that studying hard may increases the chance of getting an attractive job). Thus humans frequently engage in "mental time travel," episodic future thinking, mental simulation of

possible plans, self-reflection, and counterfactual reasoning, which support a genuinely future-oriented form of action selection (Baumeister, Masicampo & Vohs, 2011). As a consequence, we are able to pursue goals that are motivated not by a current need but by the mere anticipation of needs that may arise in the future (as when, for instance, we carry water on a strenuous hike on a hot summer's day in anticipation of becoming thirsty later, though we are not thirsty *now* and carrying the water increases energy expenditure) (Kuhl & Goschke, 1994).

Language, Inner Speech, and Verbal Intention Representations

A most remarkable feature of voluntary actions is their flexibility. In contrast to instrumental conditioning, which may require hundreds of trials to establish a novel behavior, humans are able to rapidly implement novel instructions and reconfigure response dispositions from one moment to the next. This flexibility depends critically on language, which enables us to encode a virtually unlimited number of arbitrary instructions and response rules (Goschke, 2003; Vygotsky, 1962). The importance of verbal self-instructions for flexibility is demonstrated by the finding that blocking inner speech by articulatory suppression impaired the ability to switch between different response rules, as indicated by greatly increased reaction time costs (Emerson & Miyake, 2003; Goschke, 2000). Moreover, prefrontal brain areas involved in inner speech appear to be recruited during preparation and switching of tasks (Gruber, Karch, Schlueter, Falkai & Goschke, 2006). A recent fMRI study (Ruge & Wolfensteller, 2010) revealed a remarkably rapid decrease of activation in lateral prefrontal cortex (PFC) during the first few trials of a novel task, indicating that prefrontal control based on verbal instructions is recruited primarily in the earliest phases of the implementation of novel response rules.

Persistence, Intention Shielding, and Self-Control

A complementary but equally remarkable property of voluntary action is *persistence*. Ever since Lewin (1927), both philosophical and psychological action theorists have stressed that intentions tend to persist until completion and exhibit a "characteristic *stability* or *inertia*" (Bratman, 1987; Holton, 2009). Consistent with this assumption, Goschke and Kuhl (1993) showed that representations of uncompleted intentions exhibit a heightened level of activation in long-term memory (the intention superiority effect) (see also Freeman & Ellis, 2003; Marsh, Hicks & Bink, 1998). Moreover, evidence demonstrates that intentions bias attention toward information relevant for their realization (Gollwitzer & Bayer, 1999; Gollwitzer &

Sheeran, 2006) and are "shielded" from competing motivational tendencies by volitional control processes (Gollwitzer & Bayer, 1999; Kuhl, 1985; Kuhl & Goschke, 1994).

Together, the evolution of these cognitive capacities has decoupled action from the immediate-stimulus situation and current-need state and given rise to the future directedness, flexibility, and persistence of voluntary action.

Intention and Action

In this section, I discuss in greater detail the role of intentions in the causation of action. Having an intention can be defined as a state in which an agent has a mental representation of a desired goal (e.g., "the light turns on") and an action plan suited to achieve the goal ("flipping the switch") and is committed to execute the action.

We usually have a strong impression that voluntary actions are caused by our conscious intentions. For instance, when I intentionally lift my arm, I have the impression that it was my conscious intention to lift the arm that caused the rising of my arm. Despite its intuitive plausibility, the assumption that voluntary actions are caused by conscious intentions has been challenged on the basis of findings allegedly showing that actions are instead caused by unconscious brain processes and the impression of conscious will is an "illusion" (Wegner, 2002).[2]

(How) Do Intentions Cause Actions?

One line of evidence against intentional causation has been instigated by Daniel Wegner's (2002) theory of apparent mental causation. According to Wegner, we have no direct access to the (unconscious) brain processes that cause our actions, but we experience conscious intentions as causes of actions when a thought that is consistent with the action occurs shortly before the action and there are no plausible alternative causes. Consistent with this assumption, research has shown that illusory feelings of agency or authorship can be induced experimentally. For instance, participants reported an enhanced impression of having control over randomly selected (i.e., objectively uncontrollable) stimuli appearing immediately after their self-chosen actions when a representation of the alleged "action-effect" was primed immediately before the action (Aarts, Custers & Wegner, 2005; Gentsch & Schütz-Bosbach, 2011; Linser & Goschke, 2007; Sato, 2009). Remarkably, this induced control illusion was obtained even if the "effect-primes" were presented subliminally and participants did not consciously recognize them as indicated by chance performance in a forced-choice

identification task (Linser & Goschke, 2007). However, while these findings clearly show that experienced agency or authorship rests on an—in principle fallible—causal attribution, from this it does not follow that this experience *always* deludes us. Rather, the process of matching predicted and actual action effects is a highly adaptive mechanism that most of the time provides us with valid information about whether or not an action or event was self-caused (Haggard, 2008; Linser & Goschke, 2007).

A second and arguably the most influential line of evidence against intentional causation originates in a seminal study by Benjamin Libet and colleagues (Libet, Gleason, Wright & Pearl, 1983). Participants were instructed to "freely" choose when to make a spontaneous finger movement while watching a rotating clock hand. After each movement, subjects reported at which position the clock hand had been when they became conscious of the urge to move (which on average was approximately 200 milliseconds before movement onset). Critically, the readiness potential (RP), a negative potential shift in the simultaneously registered electroencephalogram (EEG), started already several hundred milliseconds *before* subjects became aware of the urge to move. The basic result was replicated by Haggard and Eimer (1999), who measured lateralized RPs as more specific indicators of the initiation of voluntary movements.

These findings instigated an ongoing debate among psychologists, neuroscientists, and philosophers, as the evidence seems to imply that conscious intentions are an epiphenomenal by-product following rather than causing the brain processes that lead to a voluntary movement. How could my intention cause my action, if "I" become conscious of the intention only after "my brain" has already made up its mind and unconsciously "decided" to act?[3]

In evaluating this conclusion, it is important to note that it rests on four critical assumptions: (i) RPs indicate neural processes underlying the preparation of a voluntary movement; (ii) averaging across trials yields an unbiased measure of RP onsets; (iii) subjects' temporal judgments are valid indicators of the time at which they became aware of the "urge to move"; and (iv) these urges represent intentions. In fact, all four assumptions have been called into question (Banks & Isham, 2009; Joordens, van Duijn & Spalek, 2002; Rigoni, Brass & Sartori, 2010; Trevena & Miller, 2002). Here I will not discuss the methodological problems of Libet's procedure (for a recent collection of relevant papers, see Sinnot-Armstrong & Nadel, 2011) but focus on the critical question of whether his findings show that intentions play no causal role, if one assumes for the sake of argument that the first three assumptions are valid.

The answer depends critically on *how* one conceives of the causal role of intentions. What Libet's results clearly disconfirm is the view that conscious intentions are *proximate* causes that trigger voluntary movements similar to the way that a push of the cue causes the billiard ball to move (cf. Juarrero, 1999). This does not, however, imply that intentions play no causal role at all. The movements of Libet's subjects clearly depended on a *prior intention* they formed when receiving the task instruction (Goschke, 2003; Mele, 2009; Pacherie, 2008). This prior intention "configured" subjects' response dispositions such that, for the duration of the task, randomly emerging response tendencies that otherwise might have been suppressed were permitted access to the motor system (Keller & Heckhausen, 1990). Once response dispositions were so configured, no additional conscious intentions or "acts of the will" were required to trigger the subsequent movements. According to this interpretation, what subjects became conscious of about 200 milliseconds before movement onset was not an intention but simply the awareness that the next movement was about to be executed.

That actions, which depend on prior intentions, can be triggered automatically when their execution conditions are satisfied is by no means an exception but has been repeatedly demonstrated in studies of subliminal priming (see Kiefer, 2007, for a review). For instance, Neumann and Klotz (1994) instructed subjects to respond with a left or right keypress to different shapes (a square and a diamond). Unbeknownst to subjects, before each target a prime stimulus (also a square or a diamond) was presented briefly and masked by subsequent target, such that it could not be discriminated above chance. The primes nevertheless activated instructed responses, as indicated by faster responses to congruent prime–target pairs (e.g., a square primed by a subliminal square) compared to incongruent pairs (e.g., a diamond preceded by a square). Response priming was eliminated when task instructions were changed such that the primes were no longer task relevant (Ansorge & Neumann, 2005). Subsequent studies extended such effects to tasks requiring categorical judgments (Kunde, Kiesel & Hoffmann, 2003) and showed that intentions induce automatic response activation even on the first trial of a novel task (Cohen-Kdoshay & Meiran, 2009).

These findings show that automatic and controlled (intentional) responses do not constitute a dichotomy between responses triggered in an obligatory manner by stimuli and responses caused by intentions. Rather, intentions "configure" subsequent automatic processes (Hommel, 2000), and automaticity can be viewed as a *continuum* ranging from responses

that depend entirely on strong preexisting stimulus-response connections and responses requiring additional decision making or the overriding of strong competing responses (Cohen, Dunbar & McClelland, 1990).

A critical boundary condition for the automatic activation of intention-dependent responses is that the current stimulus information together with the instruction unambiguously specifies the correct response, such that no further decision making is required, and no competing responses are activated (Neumann & Klotz, 1994). Provided these conditions are satisfied, even relatively complex goal-directed actions can apparently be triggered directly by situational cues, as shown in numerous studies of so-called *implementation intentions*, which link actions to specific execution conditions (Gollwitzer & Sheeran, 2006).

An Alternative Conception of Intentions: Internal Constraints and Structuring Causes

A more general implication of the foregoing discussion is that—to use a distinction introduced by the philosopher Fred Dretske (1988)—intentions are not *triggering* but *structuring* causes. Intentions do not cause particular actions, but they are causal preconditions explaining why a particular stimulus triggers a particular action (rather than a different action). Intentions can thus be conceived of as internal *constraints* that modulate the readiness of particular response dispositions and thereby bias which responses will be activated by subsequent stimuli (Goschke, 2003). In terms of the billiard metaphor introduced earlier, intentions do not correspond to the push of the cue that sets the ball into motion, but their effect is analogous to a deformation of the billiard table's surface, which determines which trajectory the ball takes when being pushed by the cue. In this sense, intentions can be said to shape the "attractor landscape" of an agent's behavioral state space (Kugler, Shaw, Vincente & Kinsella-Shaw, 1990).[4]

The proposed account of intentions is consistent with and integrates various related theoretical proposals. For instance, in classical "will psychology," Narciss Ach (1910) already proposed that intentions establish temporary condition-action links, such that responses consistent with the intention are subsequently initiated "without a conscious recollection of the task or the instruction" (p. 150; translation mine). In a similar vein, Neumann and Prinz (1987) suggested that intentions increase the readiness of specific condition-action rules, while Hommel (2000) used the term "prepared reflex" to denote that stimulus-response bindings, once established by an intention, support the automatic transformation of stimulus information into response activation. Likewise, according to Kunde, Kiesel

and Hoffmann (2003), "action trigger hypothesis" responses are automatically activated by stimuli that match the execution conditions specified by an instruction.

On a neurocomputational level, the account of intentions as constraints fits with neural-network models of cognitive control, in which goals or task rules are represented as self-sustaining activation patterns over interconnected neurons (Miller & Cohen, 2001; O'Reilly, 2006). In these models, response activation depends jointly on slowly changing stimulus-response connections (structural constraints) and on actively maintained activation patterns representing the current goal (activation-based constraints). Importantly, neurons encoding goal representations do not directly activate response units but bias the competition between competing representations in perceptual processing pathways such that goal-relevant information gains a stronger impact on response activation and task-irrelevant information is overridden. This mechanism fits with the view of intentions as constraints that modulate the attractor landscape of the network's state space. Moreover, it is consistent with neurophysiological evidence from single-cell recordings and neuroimaging studies indicating that goals and task rules are encoded as neural activation patterns in the prefrontal cortex and modulate top-down the competition between perceptual representations in posterior brain areas toward goal-relevant information (Chadick & Gazzaley, 2011; Desimone & Duncan, 1995; Sakai, 2008).

Conflict and Volitional Control

In contrast to voluntary actions that are activated directly by stimuli, many real-life intentions cannot be realized automatically, because they stand in conflict with competing habitual or emotional responses and therefore require additional cognitive control processes. The term *cognitive control* denotes a set of mechanisms that configure processing in sensory, affective, motivational, and motor systems according to superordinate goals and serve to inhibit otherwise stronger habitual or emotional responses (Miller & Cohen, 2001). In this section, I briefly discuss some of the mechanisms and neural systems supporting the realization of intentions in cases of conflict.

Conflict and Cognitive Control

It has long been assumed that conflicts between competing responses or contradictory sources of information trigger the recruitment of cognitive

control to shield a current intention from distraction. For instance, Ach (1910) formulated a "difficulty law of motivation," according to which conflicts between intentions and habits automatically induce an intensification of "volitional effort." Likewise, Kuhl (1985, 2000) in his theory of action control assumed that conflicts lead to the mobilization of volitional control strategies. In current cognitive neuroscience, the most influential elaboration of this idea is the conflict-monitoring theory by Botvinick and colleagues (Botvinick, Braver, Barch, Carter & Cohen, 2001). The central assumption is that the anterior cingulate cortex (ACC) in the medial prefrontal lobe is part of a conflict-monitoring system that registers response conflicts and signals the demand for enhanced control to the dorsolateral prefrontal cortex (dlPFC), which mediates increased shielding of the current goal and enhanced top-down biasing of perceptual processing.[5]

Behavioral evidence for the conflict-monitoring theory stems from conflict tasks such as the flanker interference task, in which participants must respond to a central target stimulus surrounded by task-irrelevant flanker stimuli. If target and flankers are mapped to incompatible responses, reaction times are increased due to a response conflict. Interference from distracting stimuli or competing responses is often *reduced* on trials immediately following a conflict (Gratton, Coles & Donchin, 1992). This so-called conflict adaptation effect, which has also been obtained in other interference tasks such as the Stroop (Kerns et al., 2004) and the Simon tasks (Fischer, Dreisbach & Goschke, 2008), indicates that conflicts trigger the recruitment of enhanced control on subsequent trials (for a review, see Egner, 2007).[6]

Moreover, in a recent EEG study (Scherbaum, Dshemuchadse, Fischer & Goschke, 2011), we showed that conflict adaptation may even occur online *within* a conflict trial itself. Participants responded to target stimuli surrounded by distracters. By letting targets and distracters flicker with different frequencies, steady-state visually evoked potentials (SSVEP) oscillating at the stimulus flicker frequencies were induced. Because SSVEP amplitudes are sensitive to variations in the allocation of attention, this allowed us to trace the dynamics of control adjustments continuously within a trial. In conflict trials (when targets and distracter activated incompatible responses), the target-related signal was increasingly enhanced, while the distracter-related signal was attenuated, indicating that conflicts induced online an increased focusing of attention. This implies that conflict adaptation effects across trials need not always reflect active recruitment of control in preparation for subsequent conflicts but may reflect passive carry-over effects of control settings established during response selection on the previous conflict trial.

Neurocognitive Mechanisms of Self-Control

In contrast to the response conflicts discussed so far, in everyday life, conflicts often arise between long-term intentions and habitual or emotional responses (e.g., when the intention to maintain a healthy diet is undermined by the craving for a tasty dessert). While it can sometimes be rational (and pleasurable) to let current needs determine one's behavior, the ability to exert self-control, that is, to delay gratification and override momentary temptations, is essential for the pursuit of long-term goals, as well as social cooperation (Hassin, Ochsner & Trope, 2010; Mischel et al., 2010). Conversely, impaired self-control increases the risk of maladaptive behaviors such as addiction, overeating, or pathological gambling (Bühringer, Wittchen, Gottlebe, Kufeld & Goschke, 2008; Heatherton & Wagner, 2011).

In recent research on the neural systems involved in self-control, a popular paradigm is the intertemporal choice task: participants are offered choices between (usually monetary) rewards differing in size and time of delivery (e.g., between five dollars now or eight dollars in one week). When confronted with such choices, subjects often prefer the immediate, smaller over the later, larger reward, even if they choose the later, larger reward when both options are delayed (e.g., five dollars in ten weeks or eight dollars in eleven weeks). Such preference reversals have been interpreted as an indication of impulsivity and a disproportional overweighting of immediate rewards, which can be modeled mathematically as a hyperbolic discounting of delayed rewards (Peters & Büchel, 2011).

However, the cognitive mechanisms and neural systems mediating self-control versus impulsivity are still a matter of debate. One influential class of models postulates two distinct valuation systems: a "reflective" system mediating long-term anticipation and cognitive control, which discounts delayed rewards only minimally, and an "impulsive" system tuned to immediate reward, which discounts future rewards steeply (e.g., Hofmann, Friese & Strack, 2009). In support of dual systems models, an fMRI study of intertemporal choice by McClure, Laibson, Loewenstein, and Cohen (2004) revealed increased activation in limbic brain areas (ventral striatum, medial orbitofrontal cortex, and posterior cingulate cortex) when choices involved immediate rewards, whereas activation in the lateral PFC and posterior parietal cortex was independent of the delay. Moreover, activation in the PFC was greater than in limbic areas when participants chose later, larger options, whereas a reverse trend occurred when participants chose earlier, smaller options. However, contrary to the dual systems hypothesis, other studies found that activity in limbic areas was not specifically related to the presence of an immediate reward but correlated with the

subjective value of both immediate and delayed rewards (Kable & Glimcher, 2010). These results suggest a single value representation (encoded in the ventromedial PFC [vmPFC] and ventral striatum) as the final common pathway for choice behavior (for a review, see Peters & Büchel, 2010b).

A possible resolution of these conflicting findings assumes that self-control does not involve a struggle between two distinct valuation systems but rests on the top-down modulation of a common value signal by long-term goals maintained in the lateral PFC. Support for this hypothesis stems from a recent fMRI study, in which hungry subjects attempting to maintain a healthy diet made choices between different food items (healthy snacks and junk foods) (Hare, Camerer & Rangel, 2009). Self-controlled choices (rejecting tasty but unhealthy food) were associated with activation in the left dlPFC. Moreover, activity in this region during self-controlled choices correlated negatively—via an intermediate region in the inferior frontal gyrus—with the response of the vmPFC to tasty but unhealthy food, presumably reflecting the decreased weight assigned to taste in computing value. Importantly, in self-controlled subjects activation in the vmPFC correlated with both the self-rated tastiness and the healthiness of food items, whereas in impulsive subjects vmPFC activation correlated only with tastiness. These results support the idea that self-control rests on the top-down modulation of a common value representation by long-term goals maintained in the dlPFC.

Although neuroimaging studies yielded valuable insights into the complex network of brain systems involved in intertemporal choice (for review, see Peters & Büchel, 2011), the specific processing mechanisms mediating self-control remain insufficiently understood. Progress is to be expected especially from studies in which candidate mechanisms such as episodic future thinking about long-term goals are experimentally manipulated and their effect on choice behavior is observed (cf. Peters & Büchel, 2010a).

Control Dilemmas

In the previous sections, I discussed cognitive mechanisms mediating the flexibility and persistence of voluntary action. However, the evolution of anticipatory and cognitive control capacities not only expanded behavioral flexibility but also increased the potential for new kinds of conflicts. I have used the term *control dilemmas* to denote that these conflicts reflect antagonistic adaptive challenges, which require a dynamic, context-sensitive balancing of complementary control functions (Goschke, 2003).

Shielding-shifting dilemma. On the one hand, goals must be shielded from competing responses or motivational tendencies. As discussed earlier, goal shielding has obvious advantages: without being able to maintain intentions in the face of competing responses, neither pursuit of long-term goals nor social cooperation would be possible. Moreover, a persisting commitment to an intention constrains subsequent action selection and reduces the requirement to reconsider the pros and cons of alternative goals before each individual action, which is impossible given limited time and resources. However, on the other hand, shielding of intentions cannot mean irreversibility. In a constantly changing world, agents must be able to flexibly switch between goals and adapt response dispositions to changing reward contingencies. Thus too rigid intention shielding can incur a cost in terms of perseveration and inflexibility.

Selection-monitoring dilemma. On the one hand, coherent action requires focusing attention on goal-relevant information and inhibiting distracting stimuli (e.g., music from a neighborhood party when working on a paper). On the other hand, it would hardly be adaptive to suppress task-irrelevant information (e.g., the smell of fire while writing) completely, but "background-monitoring" mechanisms are required by which ignored information is processed to a level at which its potential significance for vital needs can be detected (Allport, 1989; Corbetta, Patel & Shulman, 2008; Gruber, Diekhof, Kirchenbauer & Goschke, 2010; Gruber et al., 2009). Thus while focused attention reduces interference and cross talk, it carries the risk of overlooking potentially significant information.

Anticipation-discounting dilemma. To attain long-term goals (e.g., staying healthy), one must be able to suppress current needs or habits (e.g., smoking). On the other hand, it would hardly be adaptive if we had the "willpower" to suppress vital needs completely or delay gratification forever. Given that future rewards are less predictable than immediate rewards, it is rational to discount the subjective value of delayed reward to a certain degree. This raises the problem of how to set an optimal discounting rate depending on the reliability or riskiness of delayed reward.

Exploitation-exploration dilemma. On one hand, agents should select actions that yielded reward in the past (*exploitation*). However, to discover such actions, one must explore previously untried actions (*exploration*). While exploitation supports selection of actions that proved rewarding in the past, it may prevent learning of even better options. Conversely, while exploration supports new learning, it can lead to volatile and risky behavior that is unconstrained by prior experience.

Plasticity-stability dilemma. A final trade-off concerns how fast learned knowledge should be updated in the light of new experiences. On the one hand, slow updating promotes the gradual acquisition of stable habits promoting fast but inflexible responses. On the other hand, rapid updating of stimulus-response associations promotes flexible adaptation to changing contingencies but can produce "catastrophic interference," because prior knowledge is overwritten by new experiences.

In the light of these control dilemmas, action control can be conceived of as a multiple constraint-satisfaction problem that requires a dynamic balancing of antagonistic requirements. Because a fixation at any one pole of a control dilemma usually has dysfunctional consequences, agents face *meta-control problems*, for instance, to decide whether to respond to conflicts with increased goal shielding or a switch to a different goal, or whether to respond to unexpected outcomes with continued exploitation of existing knowledge or exploration of novel options. Despite considerable progress in research on specific control processes, little is known about how the balance between complementary control processes is regulated and which factors influence how meta-control problems are solved. In the remainder of this chapter, I briefly discuss three lines of recent research on (i) complementary costs and benefits of different control modes, (ii) influences of emotions on complementary control processes, and (iii) the role of neuromodulatory systems in the adaptive regulation of cognitive control.

Costs and Benefits of Goal Shielding

A central prediction of the control dilemma theory is that antagonistic control processes incur complementary costs and benefits. For instance, whereas increased goal shielding in response to conflicts should improve performance if task rules stay constant, it should incur a cost when one must switch to a different task. Consistent with this prediction, it has been shown that enhanced goal shielding triggered by conflicts increased reaction time costs when subjects had to switch between tasks (Brown, Reynolds & Braver, 2007; Goschke, 2000; Meiran, Hsieh & Dimov, 2010).

Likewise, as predicted by the selection-monitoring dilemma, Goschke and Dreisbach (2008) showed that conflict-triggered focusing of attention impaired background monitoring for potentially relevant stimuli. Participants performed a primary task (responding to the direction of arrows, which pointed in one of four directions and appeared at one of four locations) and had in addition to press the space bar in response to a rarely occurring prospective memory (PM) cue (an arrow appearing at one particular location).

PM cues appearing on trials of the primary task that involved a response conflict (e.g., when an up-pointing arrow appeared at a lower location) were overlooked significantly more often than PM cues on trials without conflict. This indicates that conflicts increased the focusing of attention on the task-relevant stimulus dimension at the expense of impaired background monitoring for PM cues.

Consistent with the control dilemma theory, these exemplary findings demonstrate that conflict-induced goal shielding is adaptive in a constant task environment but incurs a cost when flexible switching or background monitoring is required. Thus while the conflict-monitoring theory discussed in the third section was an important step toward a mechanistic account of how cognitive control is regulated, it does not explain how meta-control problems are resolved (for instance, whether to respond to recurring conflicts with increased goal shielding or with exploration of alternative options).

Emotional Modulation of Cognitive Control

Whereas cognitive control is often studied separately from emotions, increasing evidence suggests that emotions modulate the balance between complementary control functions (for a review, see Bolte & Goschke, 2010). For instance, Dreisbach and Goschke (2004) found that positive affect facilitated set switching but at the same time increased distractibility. Participants responded to target stimuli in a particular color (e.g., red) while ignoring distracters in a different color (e.g., green). In a *perseveration condition*, after a series of trials participants had to switch attention to targets in a novel color (blue) and ignore distracters in the previous target color (red). In this condition, strong goal shielding should increase perseveration and switch costs, whereas weak goal shielding and a bias toward novel stimuli should facilitate switching. Conversely, in a *distractibility condition* participants had to switch attention to targets in the previously irrelevant color (green) while ignoring distracters in a new color (blue). Here weak goal shielding and a novelty bias should increase interference from novel distracters. As predicted by the control dilemma theory, positive affect (induced by affective pictures presented briefly before each trial) reduced switch costs in the perseveration condition at the expense of increased switch costs in the distractibility condition.

Consistent with these findings, subsequent studies showed that positive affect facilitated performance when a goal maintained in working memory unexpectedly had to be switched (Dreisbach, 2006; van Wouwe, Band & Ridderinkhof, 2011). Moreover, positive affect was associated with a broadened scope of spatial attention, as indicated by increased interference from

distracters in a flanker task (Rowe, Hirsh & Anderson, 2007). Conversely, positive affect *improved* performance in tasks requiring a broad scope of attention and access to remote semantic associates (Bolte, Goschke & Kuhl, 2003; Rowe et al., 2007). Taken together, these findings extend in important ways previous evidence on positive affect and cognitive flexibility (e.g., Isen, 2007) by showing that positive affect exerts opposite effects on complementary control functions (as predicted by the control dilemma theory).

Meta-control Parameters and Neuromodulatory Systems

Little is known about computational mechanisms and neural systems mediating the emotional modulation of complementary control functions. Computationally, control dilemmas can be related to a small set of *meta-control parameters*, which regulate global aspects of the mode of information processing (for related concepts, see Dörner, 2002; Doya, 2008). Examples of meta-control parameters are

- the *updating threshold*, which regulates the balance between maintenance and updating of goal representations (shielding-shifting dilemma);
- the *attention breadth*, which regulates the balance between focused attention and background monitoring (selection-monitoring dilemma);
- the *temporal discounting rate*, which determines how steeply delayed reward is discounted (anticipation-discounting dilemma);
- the *noise level*, which modulates the balance between exploration and exploration (exploitation-exploration dilemma);
- the *learning rate*, which determines how rapidly previous knowledge is changed by new experiences (plasticity-stability dilemma).

On a neural level, increasing evidence suggests that meta-control parameters are linked to the activity of neuromodulatory systems. For instance, the balance between stable maintenance and flexible updating appears to depend on interactions between the PFC and basal ganglia under the modulating influence of ascending dopaminergic (DA) systems (for reviews, see Cools, 2008; van Schouwenburg, Aarts & Cools, 2010). According to a current working hypothesis, an optimal DA level in the PFC promotes robust maintenance and renders PFC representations resistant against interference, whereas too low or high DA levels lead to fragile PFC representations that are prone to interference. More specifically, Durstewitz and Seamans (2008) proposed a neural-network model of PFC functioning, which postulates two distinct control modes: a D1-class receptor dominated state characterized by high barriers among different attractor states, which promotes robust maintenance but impairs set shifting; and a D2-dominated state characterized by a low

barriers between attractor states, which promotes flexible switching between representational states but also increases interference.

Complementary to the role of DA in the PFC, phasic activity of DA neurons in the basal ganglia (elicited, for instance, by reward cues) has been related to flexible updating. According to a dynamic gating hypothesis, DA projections from the basal ganglia to the PFC are involved in gating access of significant or novel information into working memory and thereby regulate the switching of cognitive sets (e.g., Montague, Hyman & Cohen, 2004; van Schouwenburg et al., 2010). Although testing these hypotheses in humans is difficult, supporting evidence was obtained in a recent pharmacological imaging study (Cools, Sheridan, Jacobs & D'Esposito, 2007), which showed that a DA receptor agonist (bromocriptine) modulated neuronal activation in the basal ganglia during cognitive set switching, whereas it modulated activation in the lateral PFC when task-relevant information had to be shielded from distracting stimuli.

Further evidence for a role of DA in regulating the flexibility-stability balance stems from studies using spontaneous eyeblink rate (EBR) as an—admittedly very indirect—indicator of central DA activity. Using the same set-switching paradigm as in our study described earlier (Dreisbach & Goschke, 2004), studies have shown that subjects showing a high EBR exhibited the same pattern of reduced perseveration and increased distractibility that we had observed after the induction of positive affect (Dreisbach et al., 2005; Müller et al., 2007; Tharp & Pickering, 2010). While these findings are consistent with the hypothesis that effects of positive affect on the stability-flexibility balance are mediated by central DA systems, currently little is known about which specific DA systems are indexed by EBRs and whether they reflect tonic or phasic DA activity.

While a more thorough discussion of the role of neuromodulators in cognitive control is beyond the scope of this chapter, it may be noted that there are indications for further links between meta-control parameters and neuromodulatory systems (for instance, the serotonin system has been implicated in modulating the temporal discounting rate [Doya, 2008], and the norepinephrine system appears to play a role in regulating the exploitation-exploration balance [Aston-Jones & Cohen, 2005]). At the same time, it must be admitted that the available evidence from human studies is at best indirect. Further research will likely show that it is oversimplified to relate single neuromodulators to specific control parameters, given that neuromodulators influence several cognitive functions, interact with one another, and differ in their effects depending on the site of action, receptor types, and baseline activity.

Conclusions and Future Directions

In this chapter, I have discussed three fundamental questions for an integrative theory of voluntary action. First, with respect to the question which role intentions play in the causation of action, I have argued for a view of intentions as internal constraints, which bias perceptual processing and response selection over extended durations. This view of intentions as structuring (rather than as triggering) causes accounts for the fact that responses that depend on prior intentions can be initiated automatically, and is consistent with evidence for the special persistence of intentions. Secondly, I discussed neurocognitive mechanisms underlying volitional control processes by which intentions are shielded from competing habitual or motivational responses. In particular, I presented evidence showing that increased goal shielding in response to conflicts does not only have beneficial effects, but can also incur costs in terms of increased switch costs and impaired background monitoring. Finally, I outlined a wider theoretical framework according to which voluntary action affords a dynamic balance between antagonistic adaptive requirements, which give rise to a set of fundamental control dilemmas. I presented evidence that metacontrol parameters regulating the balance between complementary control functions (e.g., stable goal shielding vs. flexible goal switching) is modulated by emotions and associated neuromodulatory systems. A more general implication of the control dilemma framework is that voluntary action does not rest on a special "volitional capacity" or unitary "executive control system" but emerges from interactions between large-scale brain systems mediating complementary control functions. This framework raises a host of unresolved questions for future research, for instance, how the balance between complementary control functions is modulated on different timescales by conflicts and emotions; how complementary control processes are adapted to statistical task features such as the predictability and volatility of rewards; how meta-control parameters relate to neuromodulatory systems and how they are moderated by individual differences and genetic variation; and by which computational mechanisms meta-control parameters are implemented.

Acknowledgments

The preparation of this chapter and the author's research reported therein were supported by the German Science Foundation (Go-720/3-2 and 3-3; SFB 940) and the Volkswagen Foundation (II/80774).

Notes

1. It is beyond the scope of this chapter to discuss the philosophical problem of free will (for overviews of current positions, see Kane, 2011). Suffice it to note that so-called libertarian theories that postulate an undetermined free will face the problem of how to distinguish voluntary actions from random events.

2. It is beyond the scope of this chapter to do justice to the complex conceptual and methodological discussions that surround the distinction between conscious and unconscious processes. For the purpose of the present argument, it suffices to note that in most of the discussed experiments, consciousness is defined operationally in terms of whether mental contents are reportable, whereas unconscious contents are either defined according to a subjective criterion as being not reportable or according to an objective criterion as being not discriminable above chance level.

3. This conclusion raises philosophical questions that are beyond the scope of this chapter. In particular, it presupposes that actions qualify as being caused by "me" only if they were not caused by brain processes, whereas actions that *are* caused by brain processes cannot be caused by *me* or my conscious intention. This argument appears to imply mind–brain dualism, raising the perennial question of how a nonphysical intention can set physical bodies into motion. This problem is avoided if one conceives of intentions as identical with, or instantiated by, particular brain processes, in which case stating that an action was caused by an intention and stating that it was caused by a brain process instantiating the intention denote the same cause on different levels of description.

4. The present account bears relationships to Pacherie's (2008) three-tiered model of intention, in which she distinguishes distal, proximal, and motor intentions. However, the point of the current proposal is not so much the temporal distance or abstractness of intentions but *how* intentions cause behavior. According to the present hypothesis, even proximal intentions (e.g., "I intend to lift my arm *now*") do not *directly trigger* movements but modulate the readiness of particular motor programs, albeit on a very short timescale.

5. The functional characterization of the ACC is a topic of debate, and apart from conflict monitoring, it has been implicated in conflict resolution, avoidance learning, and effort estimation (Mansouri, Tanaka & Buckley, 2009).

6. Alternative interpretations attribute sequential congruence effects to repetition priming (Mayr, Awh & Laurey, 2003) or feature binding (Hommel, Proctor & Vu, 2004). Various attempts to disentangle these effects from conflict-induced control adjustments suggest that both kinds of processes contribute to sequential modulations of congruence effects (for a review, see Egner, 2007).

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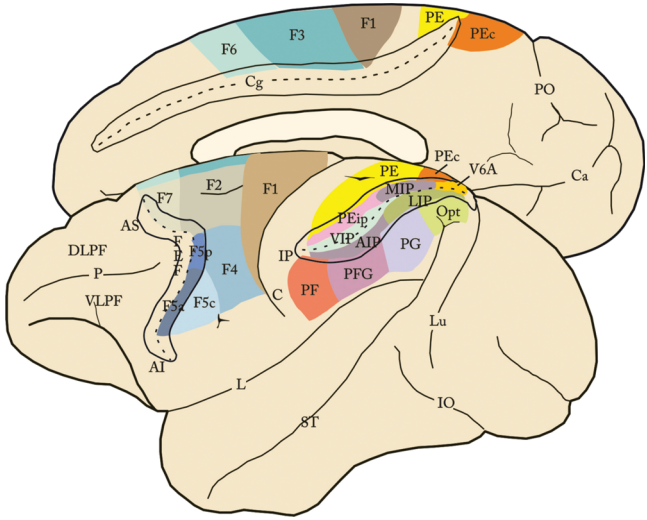

Plate 1 Mesial and lateral views of the macaque brain showing the cytoarchitectonic parcellation of the frontal motor cortex (areas indicated with *F* and Arabic numbers) and the parietal lobe (areas indicated with *P* and letters). Areas buried within the intraparietal sulcus (IP) are shown in an unfolded view of the sulcus. AIP, anterior intraparietal area; As, superior arcuate sulcus; Ai, inferior arcuate sulcus; C, central sulcus; Ca, calcarine fissure; CG, cingulate cortex; DLPF, dorsolateral prefrontal cortex; VLPF, ventrolateral prefrontal cortex; FEF, frontal eye field; F5a, anterior sector; F5c, convexity sector; F5p, posterior sector; IP, intraparietal sulcus; L, lateral sulcus; LIP, lateral intraparietal area; MIP, medial intraparietal area; Lu, lunate sulcus; Opt, occipito-parieto-temporal area; P, principal sulcus; POs, parieto-occipital sulcus; STS, superior temporal sulcus; VLPF, ventrolateral prefrontal cortex; V6a, anterior area V6.

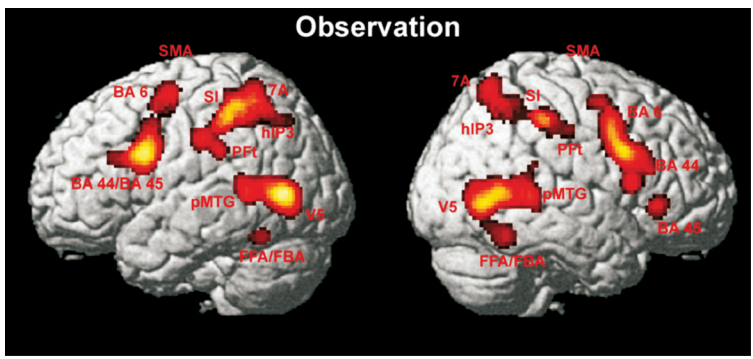

Plate 2 Cortical areas active during action observation in humans. Lateral view of the two hemispheres of a human brain showing the areas activated in neuroimaging studies during action observation. Data from a meta-analysis made on 87 studies. The three main nodes of the action observation circuit are the posterior part of the superior temporal sulcus; the inferior parietal lobule, including the intraparietal sulcus, plus the adjacent part of superior parietal lobule; the premotor cortex, mainly its ventral part, plus the posterior part of the inferior frontal gyrus (modified from Caspers, S., Zilles, K., Laird, A. R., Eickhoff, S. B. [2010]. ALE meta-analysis of action observation and imitation in the human brain. *NeuroImage*. 50, 148–167. © Elsevier 2009, with permission from Elsevier).

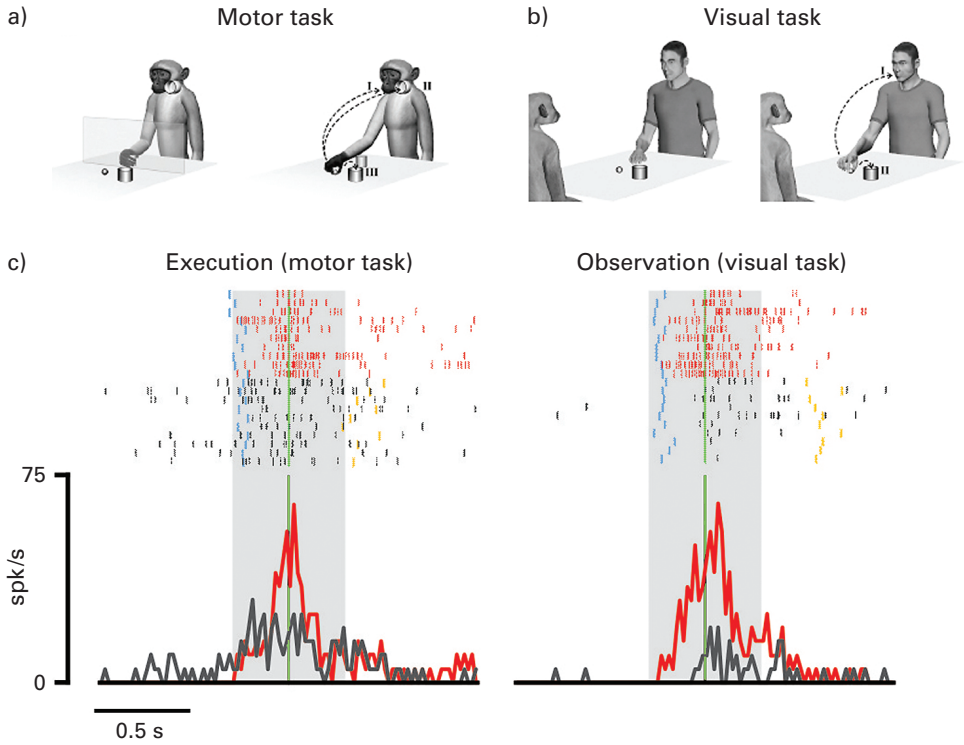

Plate 3 Example of an F5 mirror neuron modulated by action intention. (a) Paradigm used for the motor task. The monkey, starting from a fixed position, reaches and grasps a piece of food, then brings it to the mouth (I, grasp-to-eat), or places it into one of the two a containers (II/III, grasp-to-place). (b) Paradigm used for the visual task. The experimenter, starting from a fixed position, reaches and grasps a piece of food, then brings it the mouth (I, grasp-to-eat) or places it into a container (II, grasp-to-place). (c) Discharge of the neuron during execution (left) and observation (right) of the two actions. Rasters and histograms are aligned (green vertical lines) on the contact between the monkey's or experimenter's hand with the object. Red: neuron discharge during grasp-to-eat condition; gray: neuron discharge during grasp-to-place condition. Blue bars indicate the onset of the hand movement; yellow bars indicate the contact between the hand and the container in the grasp-to-place condition (modified from Bonini, L., Rozzi, S., Serventi, F. U., Simone, L., Ferrari, P. F. & Fogassi L. [2010]. Ventral premotor and inferior parietal cortices make distinct contribution to action organization and intention understanding. *Cerebral Cortex*, 20, 1372–1385, by permission of Oxford University Press).

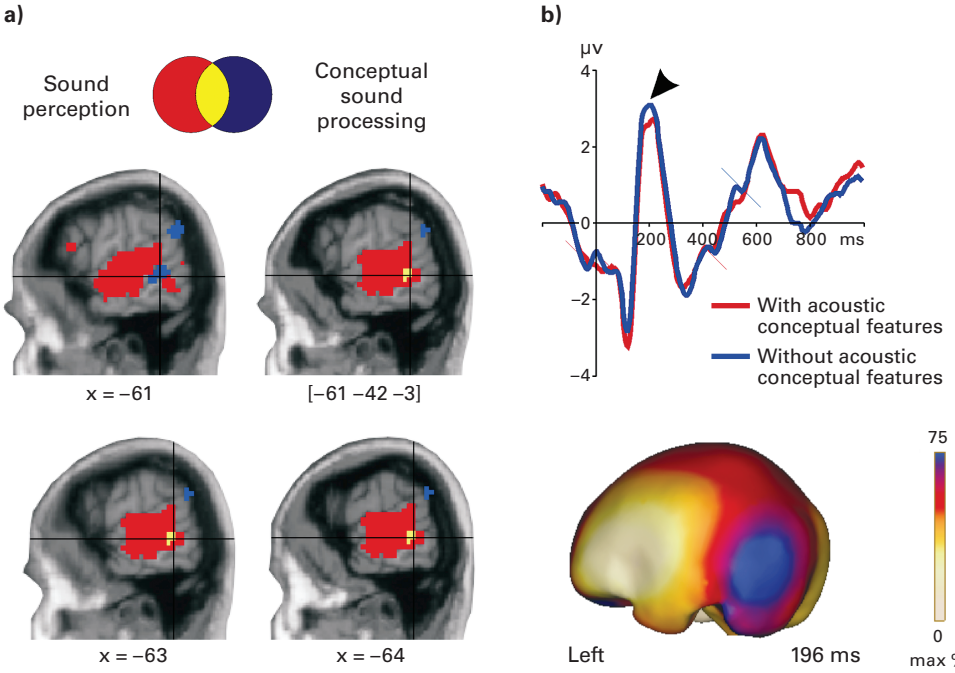

Plate 4 The grounding of concepts in auditory brain systems. (a) Functional-anatomical overlap between conceptual and perceptual processing of acoustic features. Increased functional activation to words with acoustic conceptual features (conceptual processing) overlaps with brain activation during listening to real sounds (sound perception) in left posterior superior and middle temporal gyrus (pSTG/MTG). Shown are contiguous slices centered on the peak coordinates. (b) Time course of conceptual processing of acoustic features. Top: Event-related scalp potentials to words with versus without acoustic features at central electrodes. Potentials are collapsed across central electrode sites. The arrow indicates the onset of the effect. Bottom: Brain electrical sources of scalp ERPs: maps of cortical currents calculated according to the minimum norm algorithm from the ERP difference waves (with versus without acoustic features). Maps are shown for the respective maxima in global field power. Strongest cortical currents (visualized in blue color) were observed in and close to left pSTG/MTG. Adapted from Kiefer et al. (2008).

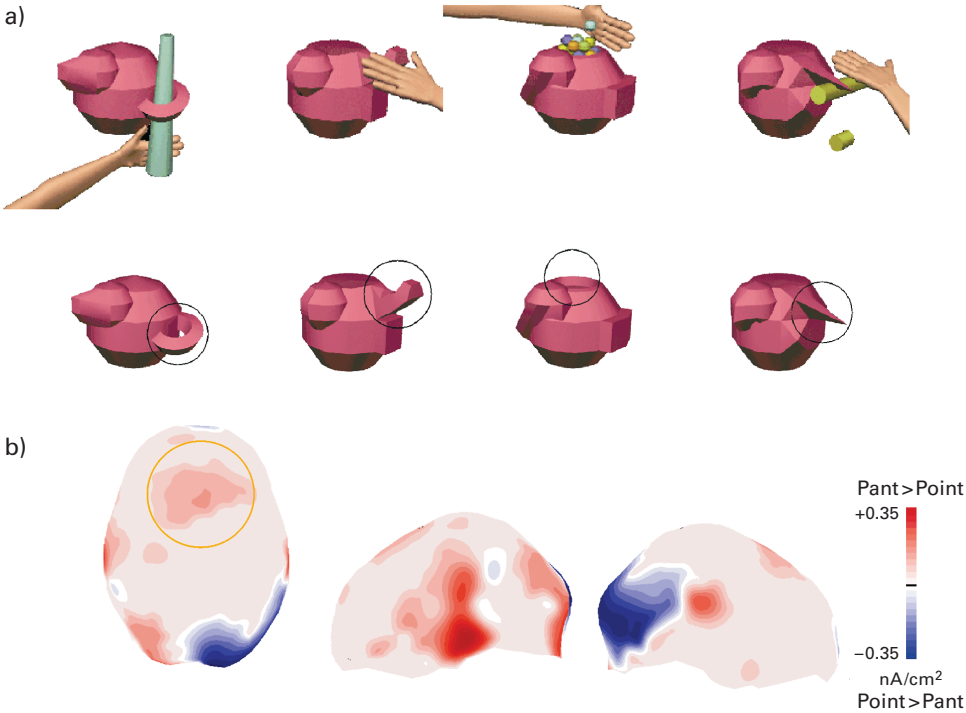

Plate 5 Experience-dependent plasticity of conceptual representations in the visuomotor system. (a) Examples of the novel 3-D objects ("nobjects"), for which conceptual knowledge was acquired during training and demonstrations of the different training conditions. Top: Actions associated with the detail feature in the pantomime training group. Bottom: Pictures highlighting the detail feature to be pointed to in the pointing training group. (b) Minimum norm source estimates obtained from grand-mean scalp ERPs at test after the training during a categorization task. Shown are difference maps between the pantomime and the pointing condition at 117 ms after picture onset. Note the fronto-central activation (yellow circle) close to the premotor cortex in the pantomime group. Adapted from Kiefer et al. (2007).