

Introduction to Section on Perception and Action

Themes in Perception and Action

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Introduction

Over the past few decades, several research communities have (more or less independently) converged onto the idea that many interesting and important issues can be addressed by studying the connection between perception and action. Although much has been learned about vision, hearing, touch, and motor control by studying these systems in isolation, investigations of the rich interplay between perception and action have led to a new set of research questions and a fresh perspective on old problems. The six chapters that follow illustrate why the study of perception and action is bound to play an important role in making *progress in motor control*.

The primary goal of this introductory chapter is to provide readers with some broader context to better appreciate the six chapters that follow. In the next section, four central themes in the study of perception and action will be reviewed: (1) the coupling of perception and action, (2) the role of internal models, prediction, and planning, (3) the two visual systems hypothesis, and (4) neural mechanisms for perception and action. Along the way, previews of the six chapters in this section of the book will be provided. Some of the goals of research on perception and action, as well as some of the theoretical and methodological approaches will be mentioned. But details will be kept to a minimum, as the main purpose of this chapter is to provide a thematic overview.

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Four Themes in Perception and Action

Perception-Action Coupling

During our daily routines, we perform numerous tasks that require us to coordinate the movements of our bodies with complex, dynamic environments. While walking along a crowded sidewalk, we pass through gaps between other pedestrians, circumvent stationary obstacles, step over barriers, potholes, and puddles, and climb stairs and ramps. On roadways, we follow traffic lanes, maintain a safe headway behind lead vehicles, and decelerate to a safe speed before entering a sharp curve. How does one go about understanding such behaviors in a way that does justice to the tight coupling of perception and action? The theoretical approach that takes the coupling of perception and action most seriously is James J. Gibson's (1986) ecological approach. What is needed here, according to those who subscribe to the ecological approach, is a theory of *direct perception* that does away with processes and entities that mediate perception and action (e.g., inferential mechanisms, mental representations, internal models) and allows for direct epistemic contact with the environment.

Information-based control. A first step toward meeting the challenge of direct perception is to identify perceptual information that specifies action-relevant properties of the environment, and to show how such information is used to control action. Consider, for example, the task of catching a ball, which requires actors to coordinate the movements of their bodies on the basis of perceptual information in order to satisfy oftentimes precise spatial and temporal demands. The *information-based* approach to the study of catching has led to the identification of optical variables that specify such action-relevant properties as when the ball will pass within range, where it will be at that point in time, and its direction of motion (see chapters in Hecht & Savelsbergh, 2004), as well as candidate control strategies that capture how such information is used to guide hand movements (Dessing, Peper, Bullock, & Beek, 2005; Michaels, Jacobs, & Bongers, 2006; Peper, Bootsma, Mestre, & Bakker, 1994). Similarly, information-based accounts of fly ball catching describes how outfielders arrive at the landing location in time to catch the ball by running so that the ball follows a particular optical trajectory, eliminating the need to estimate landing location (Chapman, 1968; McBeath, Shaffer, & Kaiser, 1995; McLeod, Reed, & Dienes, 2006; Michaels & Oudejans, 1992). Thus, the ecological, information-based approach aims to capture perception-action coupling by identifying action-relevant informational variables, and task-specific control strategies that describe how variables on the information side map onto variables on the action side (see Warren, 1988, 1998 for reviews).

Affordances. From an ecological perspective, the notion of direct perception extends to a class of properties, known as *affordance*, that are characterized as the possibilities (or opportunities) for action provided by the environment.

Thus, the theory of affordances states that actors can directly perceive what actions are possible and what actions are not possible. Indeed, the empirical research on affordance perception, originating with the classic work on the perception of stair climb-ability by Warren (1984), has revealed that actors can perceive a variety of affordances with remarkable accuracy (see Fajen, Riley, & Turvey, 2007 for a recent review). The contribution by **Carello and Wagman** in this volume illustrates how the theory of affordances has been applied to the study of dynamic touch. Dynamic touch provides us with an impression of the properties of objects and limbs by means of our wielding them, and plays a critical role in countless routine activities that involve the coordination of limbs, tools and implements, and other objects. The authors show that a number of action-relevant properties (i.e., affordances) can be directly perceived by means of dynamic touch. This is illustrated using the affordance of *move-ability*, an action-relevant re-characterization of the standard property that we often call *heaviness*. Whereas heaviness is associated with an object's weight, move-ability can be captured in terms of the object's resistance to being moved, which is quantified by the inertia tensor. Interestingly, when subjects are asked to estimate heaviness, their judgments turn out to be a single-valued function of the inertia tensor that reflects the object's resistance to being moved; in other words, judgments are based on the action-relevant property that is specified by the information. These and many other findings from the study of dynamic touch are integrated by Carello and Wagman into a broader theoretical framework that offers a compelling case for the direct perception of affordances.

Information and dynamics. Finally, the notion of perception-action coupling is also quite compatible with the dynamical systems approach to coordination. From the dynamics perspective, actor and environment are coupled both mechanically and informationally, and behavior emerges from the actor-environment system as the actor learns information-movement mappings that exploit the intrinsic dynamics of the system (see Warren, 2006 for a tutorial-style review that integrates information-based control with the dynamical systems approach). For example, a complex skill like rhythmically bouncing a ball on a paddle can be performed by exploiting a dynamically stable solution that eliminates the need for active error corrections (Sternad, Duarte, Katsumata, & Schaal, 2001). However, both visual and haptic information play important roles in moving the system into the passively stable region, and keeping it there.

Internal Models, Prediction, and Planning

The ecological, information-based approach to understanding the coupling of perception and action continues to provide the inspiration for a great deal of work on the perceptual control of action. At the same time, there are

ways to formulate the problem of perceptual control of action without assuming a tight linkage between information and movement. Loomis and Beall (2004) described a general theoretical framework, which they call *model-based control*, that relies heavily on mental representations of the environment constructed from perceptual cues. Empirical support for model-based control is largely derived from studies of *visually directed action*, in which actors view a scene, close their eyes, and perform the required action (e.g., Philbeck, Loomis, & Beall, 1997). The reliability and accuracy of performance is interpreted as evidence that actors construct a mental representation of the environment that is sufficiently accurate and detailed to support action.

Lacquaniti and colleagues (see Zago & Lacquaniti, 2005 for a review) proposed that internal models of the environmental dynamics play a critical role in catching and hitting, two tasks that are often assumed to reflect the tight coupling of perception and action. The information-based account is challenged on the grounds that the brain must rely on an internal model of gravity to time interactions with falling objects. In a series of studies using clever manipulations and detailed analyses, these researchers have accumulated convincing evidence that actions are timed in ways that take into account the effects of gravity. Such findings were interpreted as evidence that the gravitational constant, a regularity that is ubiquitous on earth, is internalized by the CNS (see also, Hayhoe, Mennie, Gorgos, Semrau, & Sullivan, 2004).

Many other lines of research that figure prominently assume critical roles for processes like *planning* and *feedforward control*, that downplay the importance of perception-action coupling.¹ An instructive example of the complementary roles of feedback and feedforward control in a perception-action task comes from the study of automobile driving (Land, 1998). Donges (1978) proposed a model of steering that included two modes of control. The compensatory, feedback mechanism corrects for errors in lane position, and primarily relies on information from the visible foreground immediately ahead of the vehicle. The other mode of control is an anticipatory, feedforward mechanism that relies on an estimate of the curvature of the road ahead, which is obtained by fixating the tangent point of the road (Land & Lee, 1994). When the estimate is accurate, the feedforward mechanism can match the curvature of the road. Small deviations in lane position can then be corrected by the feedback mechanism. Because most of the work is done by the feedforward mechanism, the feedback mechanism can operate at low gain to avoid instabilities that arise when the feedforward mechanism is impaired, as occurs when distant segments of the road needed to estimate road curvature are occluded (Land & Horwood,

¹ Because the use of these concepts is widespread in motor control, and many readers of this volume are likely to be familiar with such work, the focus here will be on the application of these ideas in the context of 'perception-action' tasks for which both the perception and motor components are non-trivial.

1995). Thus, feedback and feedforward control work together to allow for stable steering control with small lane position error.

In the present volume, the issue of feedback and feedforward control is taken up in the chapter by **McVea and Pearson**. In the first part of that chapter, the authors provide an integrative summary of behavioral studies on the role of visual information during locomotion in humans and quadrupeds. The specific focus is on the guidance of leg movements when foot placement is constrained or when stepping over obstacles. Evidence from a number of studies supports the assertion that visual information is used to guide leg movements in a feedforward rather than feedback manner. Thus, obstacles that lie along the future path are sampled a few steps before they are crossed, and such sampling is sufficient to plan and control locomotion. Ongoing, continuous visual feedback is not necessary to guide the legs over recently sampled obstacles. Studies of cats stepping over obstacles provide a consistent story, leading the authors to conclude that quadrupeds rely on a detailed and persistent form of visuo-motor memory that plays an important role in guiding the hindlegs over obstacles without visual feedback. In the second part of this chapter, the authors tie these behavioral findings together with what is known about the neurobiology of visually-guided stepping.

An important take-home message of the chapter by McVea and Pearson is that visual information is used to plan leg movements in advance. The role of visual information in planning reaching movements of the arm is the focus of the chapter by **Sarlegna and Sainburg**. Specifically, the authors evaluate the contributions of both visual and proprioceptive information about arm configuration to the planning of reaching movements. Although both modalities provide information about arm configuration, they appear to contribute differently to the planning of arm movements. Vision provides information about limb and target position in an extrinsic reference frame, and is used to create a kinematic plan for movement. Proprioception provides information about arm configuration that is necessary to transform the kinematic plan into motor commands that generate the forces necessary to move the arm. Evidence from a variety of different sources, including work on both normal subjects and patients, is integrated to provide support for this hypothesis.

Continuing with the theme of predictive mechanisms, the chapter by **Stanley and Miall** builds upon previous work on the role of forward modeling in the perceptual control of action (e.g., Mehta & Schaal, 2002; Miall & Jackson, 2006). Forward modeling is a process in which the current sensory information is combined with information about motor commands to generate a prediction about the future state of a segment of the body. Stanley and Miall address the question of whether the output of this predictive process is available to non-motor processes. Specifically, they investigate a phenomenon called “motor-visual priming,” in which the preparation of a motor response yields a prediction of the outcome of the response in terms of sensory consequences, which in turn facilitates performance on a visual discrimination task. The chapter describes a

series of experiments using a clever methodology designed to test for evidence of motor-visual priming. In the final section, the authors describe a fMRI study indicating that the motor-visual priming effect is localized to the superior PPC, one area where the integration of visual information and motor efference copy is thought to take place.

Vision-for-Perception Versus Vision-for-Action

Among the most influential recent developments in perception and action is the so-called *two visual systems hypothesis*, first proposed by Goodale and Milner (1992). A few of the many reviews of this work are Milner and Goodale (1995), Goodale and Milner (2004), and Goodale and Westwood (2004). Before going any further, it is important to recognize that the terms ‘perception’ and ‘action’ are used in a particular way in this line of research, that differs to some extent from the way in which they are used elsewhere. This is another indication of the diversity of approaches in the study of perception and action. Proponents of the two visual system hypothesis use these terms to refer to two distinct functions served by the visual system. Perception refers to the rich, detailed representation of the environment that is accessible to conscious visual awareness, and plays a critical role in recognition and identification. Action refers to the guidance of movement on the basis of vision. Thus, the visual system can provide us with an awareness of the environment, and it can provide us with a means by which to control our actions. Milner and Goodale’s fundamental claim is that these two functions are carried out in distinct, independent processing streams in the primate visual system. Vision-for-perception is carried out in the ventral stream, which projects from the early visual areas to the temporal lobe. Vision-for-action is carried out in the dorsal stream, which projects from the early visual areas to the parietal lobe.

The two visual systems hypothesis has had a significant impact on the study of vision because it challenges the conventional view that vision-for-perception and vision-for-action are one and the same. Research in this area focuses on finding evidence to support, refute, or refine the original two visual systems hypothesis. Much of the early evidence comes from studies of patients with brain damage to either the dorsal or ventral stream. Although the pattern of deficits varies from patient to patient, some individuals with damage to the ventral stream exhibit degraded performance on perceptual judgment tasks but normal behavior on visually guided actions. Conversely, those with damage to the dorsal stream exhibit the opposite pattern of performance. More recently, fMRI studies have been conducted to localize the damage in these patients, and monitor activation in the dorsal and ventral streams as these different tasks are performed. Others have sought behavioral evidence in normal, healthy subjects with intact visual systems by looking for dissociations between performance on

perceptual judgment tasks and visually guided actions (Aglioti, DeSouza, & Goodale, 1995).

Neural Mechanisms

Studies of neural mechanisms add another dimension to the idea that perception and action interact in interesting ways. Recent work on the neural mechanisms underlying visually guided locomotion (McVea and Pearson, this volume), reaching (Culham & Valyear, 2006), and interception (Merchant & Georgopoulos, 2006), as well as the detection of action-relevant information in optic flow (Duffy, 2003; Frost & Sun, 2004) are just a few of the many excellent examples. In addition to the chapter by McVea and Pearson, two other chapters in this section address issues related to the neural basis for perception and action.

The mirror neuron system. An exciting development in neuroscience with potentially far-reaching implications is the discovery of the mirror neuron system, which is the focus of the chapter by **Aziz-Zadeh and Ivry** (see also, Rizzolatti & Craighero, 2004; Rizzolatti, Fogassi, & Gallese, 2006 for recent reviews). Mirror neurons are visuomotor neurons found in the premotor and parietal areas that fire in response to specific goal-directed actions, both when the animal performs the action and when it observes the action performed by another animal. Thus, a particular mirror neuron might fire both when a monkey grasps a piece of food and when the same monkey watches another monkey (or a human) grasp the piece of food. Much of the research on this topic is aimed at further understanding the basic properties of mirror neurons in both monkeys and humans. Aziz-Zadeh and Ivry provide a summary of some of this work, and go on to explain why the discovery of the mirror neuron system has generated so much excitement. Mirror neurons provide a possible neural mechanism for the comprehension of the goals of another person's actions, and may play critical roles in speech perception, and learning by imitation (Iacoboni, 2005). It has also been suggested that dysfunction of this system may be implicated in autism (Ramachandran & Oberman, 2006). Aziz-Zadeh and Ivry remind us that the fact that mirror neurons reside in so-called motor areas is yet another indication that carving the brain into perceptual regions and motor regions is too simplistic. In this sense, the study of mirror neurons helps shape our understanding of the link between perception and action.

Deficits and disorders of perception and action. Our understanding of the neural mechanisms involved in the perceptual control of action has benefited from the study of patients with neurological deficits. The chapter by **Jax and Coslett** nicely summarizes recent research on three disorders of the perceptual-motor system: disorders of the body schema, optic ataxia, and ideomotor apraxia. They make a strong case for why our understanding of fundamental issues in motor control and perception and action can benefit from the study of

patients with disorders of the perceptual-motor system (and vice-versa). Studies of patients with disorders of the body schema reveal important clues about how actors maintain a representation of the configuration of the body, the neural mechanisms involved in generating such representations, and the role of these representations in producing movements. Studies of patients with optic ataxia provide insight into the transformations among coordinate frames involved in visual control, and the distinction between motor planning and online control. The study of ideomotor apraxia has provided a convenient way to address central issues in motor control, including the role of stored representations of movements, the use of extrinsic and intrinsic reference frames, and the distinction between movement planning and control.

Conclusion

Although its origins can be traced back to developments that are now several decades old, perception and action is still a rapidly developing area of research. To a large extent, such growth can be attributed to the increasing number of research groups that have adopted the perception-action perspective. Indeed, no single community of researchers can claim to own the topic of perception and action, and the diversity of goals and theoretical and methodological approaches represented in this section of the book is an indication of that fact. Such diversity has dramatically broadened the scope of research that is encompassed by perception and action, and extended the reach of its implications to include vision science, motor control, developmental psychology, rehabilitation, sports sciences, robotics, human factors, and so on. It is expected that the six chapters that follow will help to contribute to the continued growth and development of this exciting area of research.

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