

Motor Cognition and Mental Simulation

Learning Objectives

1. The Nature of Motor Cognition
 - 1.1. Perception–Action Cycles
 - 1.2. The Nature of Motor Processing in the Brain
 - 1.3. The Role of Shared Representations
2. Mental Simulation and the Motor System
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 - 4.1. The Perception of Biological Motion
 - 4.2. Processing Biological Motion
 - 4.3. Motor Cognition in Motion Perception

Revisit and Reflect

It's late at night. You've taken a break from a demanding reading assignment and picked up a detective story . . .

In front of us as we flew up the track we heard scream after scream from Sir Henry and the deep roar of the hound. I was in time to see the beast spring upon its victim, hurl him to the ground, and worry at his throat. But the next instant Holmes had emptied five barrels of his revolver into the creature's flank. With a last howl of agony and a vicious snap in the air, it rolled upon its back, four feet pawing furiously, and then fell limp upon its side. I stooped, panting, and pressed my pistol to the dreadful, shimmering head, but it was useless to press the trigger. The giant hound was dead.

It's Watson who hears the frightful cries, Watson who is running with Holmes across the moor, Watson who is panting—and the hound of the Baskervilles is no threat to you, safe in your room. But as you come to the climax of the story you realize that *your* pulse is racing, *your* heart is pounding; physical, motor responses are being evoked by imaginary stimuli. What's going on?

What's going on is that imagining the actions of another person, even a fictional other person, and taking that person's perspective of events recruit some of the same mental processing and activate some of the same neural networks as would be activated if you really were experiencing the imagined situation. In the previous chapter we discussed problem solving and reasoning of the sort that largely rely on conceptual analyses; in this chapter, we discuss another way in which thinking occurs that relies on mentally simulating possible actions or events. Historically it was thought that such simulations were used by young children prior to conceptual thought, and thus much of the relevant research we consider in this chapter will focus on development.

What would you have done if you were Watson? To answer this question, you might “put yourself in his shoes,” imagining how you would react if you were in his place. Such thinking relies on motor cognition; **motor cognition** is mental processing in which the motor system draws on stored information to plan and produce our own actions, as well as to anticipate, predict, and interpret the actions of others. Throughout this chapter we investigate and provide evidence for the claim that some sorts of reasoning and problem solving rely on motor cognition, which often uses mental imagery to run “mental scenarios” that allow you to “see what would happen if. . . .” We specifically address these overarching questions:

1. What is the nature of motor cognition?
2. What is a mental simulation of action?
3. Why and how do we reproduce the actions of others?
4. What is the role of motor cognition in perception?

1. THE NATURE OF MOTOR COGNITION

You may never have thought much about how you plan and control your movements, but even a moment's reflection should make you aware that your actions typically are not reflexes, triggered by an external stimulus (such as occurs when you yank your hand back from a hot stove), but rather are the visible manifestation of a series of mental processes. A key idea is that these same mental processes can be used in cognition, even when they do not result in a specific movement. To see how the processes used to plan and guide movement can also be used in reasoning and problem solving, we must begin by considering the nature of motor processing.

Many contemporary researchers assume that there is a continuity between planning and enactment. In this view a **movement** is considered to be a voluntary displacement of a body part in physical space, whereas an **action** is a series of movements that must be accomplished in order to reach a goal. Indeed, actions are planned with respect to a specific goal. For example, if you are thirsty and want to take a sip of coffee, you might look at your coffee mug, reach toward it, wrap your

fingers around the handle, lift the mug, and bring it to your lips. Motor cognition encompasses all the mental processes involved in the planning, preparation, and production of our own actions, as well as the mental processes involved in anticipating, predicting, and interpreting the actions of others.

1.1. Perception–Action Cycles

A key to understanding the nature of motor cognition is the concept of the **perception–action cycle**, which is the transformation of perceived patterns into coordinated patterns of movements. For example, you casually notice how high each step in a stairway rises, and you lift your feet accordingly (Gibson, 1966). As we shall see, even this seemingly very simple sort of movement planning—unconsciously figuring out when and how high to lift your feet—relies on a sophisticated set of neural processes. Evolutionarily speaking, perception exists not just to recognize objects and events, but also (as noted in Chapter 2), to provide guidance and feedback for the many different movements that animals make, so that a given movement is efficient and successful in its aim. Moreover, it is not just that perception exists partly in the service of planning movements; our movements allow us to perceive, which in turn allows us to plan our subsequent movements. Animals move so that they can obtain food, and eat so that they can then move; they move so that they can perceive, and perceive so that they can move. Perception and action are mutually intertwined and interdependent—and motor cognition lies at the heart of how the two interact. We plan so that we will reach an action goal, and what we perceive lets us know whether we are getting closer to that goal, or are on the wrong track.

What is the mediating link between perception and action? Neurophysiological and behavioral evidence suggests that the link is representation: that there is shared coding in the brain of perception and action, and that the contents of both perceptions and **intentions**—mental plans designed to achieve a goal through action—depend on neural processes with both perceptual and motor aspects (see Haggard, 2005).

1.2. The Nature of Motor Processing in the Brain

We have stressed that motor cognition is grounded in the systems used to control movement. A fundamental fact is that different brain areas support different motor processes. We focus on three motor areas; evidence for their roles in information processing comes in large part from the effects of experimental lesions in animals (Passingham, 1993) and clinical observations of humans with brain damage. Area M1 (discussed in Chapter 1) is the “lowest level” motor area; neurons in this area control fine motor movements, and send fibers out of the brain to the muscles themselves. The premotor area (PM) is involved in setting up programs for specific sequences of actions (and sends input to M1), and the supplementary motor area (SMA) is involved in setting up and executing action plans. Thus, these areas are often regarded as forming a hierarchy, with M1 at the bottom and SMA at the top. For our present purposes we cannot go too far wrong by considering the areas as processing increasingly abstract sorts of information, from specific movements (M1)

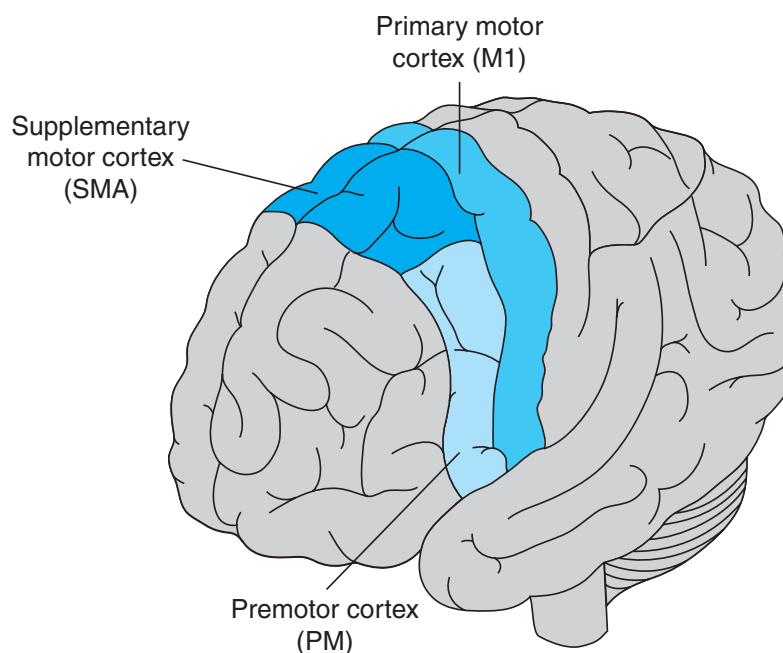


FIGURE 11–1 Key cortical motor areas

Three brain areas used in motor control and motor cognition.

(Figure based on <http://www.brainconnection.com/med/medart/1/motor-cortex.jpg> showing only primary motor cortex (M1), premotor cortex (PM) and supplementary motor cortex (SMA).)

to less precisely specified sets of movements (PM), to overarching plans for action (SMA). These three areas are illustrated in Figure 11–1.

Here is some evidence for the distinct roles of the three areas. Several studies have compared neuronal activity in M1, PM, and SMA during preparation of motor responses to investigate the distinction between processing of externally generated tasks (for example, reaching to turn off your alarm clock) and internally generated ones (for example, setting your alarm clock). In the latter case, you need to plan in advance; in the former case you do not. Mushiake and colleagues (1991) recorded single-cell activity in M1, PM, and SMA of monkeys immediately before and while they were carrying out a sequential motor task. The key to the experiment was that a movement sequence was either visually triggered (VT) or internally triggered (IT). In the VT condition, monkeys were required to touch three pads on a panel as they were illuminated in a random sequence. In the IT condition the monkeys were required to remember a predetermined sequence and press it on a keypad without visual guidance.

The results showed that most M1 neurons exhibited similar activity during both premovement and movement periods, in both the IT and VT conditions. This makes sense, because the same movements ultimately were produced in the two conditions. However, in SMA more neurons were active in the IT condition than in the VT condition during both the premovement and movement periods, which suggests that having to formulate a plan involves SMA. In contrast, in PM more neurons were active during the VT than the IT condition in both periods, which suggests that this area is involved in setting up specific movement sequences. These findings show that

motor production as a whole—premovement and movement—exists at a number of levels of processing; moreover, neural processing differs when you are formulating a plan in advance and when you are simply responding to an environmental cue.

The discovery that these three brain areas operate on increasingly more specific information might suggest that the areas always operate strictly in sequence; specifically, it might be tempting to think that SMA finishes processing and only then directs PM, which finishes its processing and only then in turn directs M1. But this apparently is not the case. Instead, other neural evidence suggests that the three brain areas do not always operate in this sequence, but instead interact in complex ways. Nevertheless, different brain regions play different roles in the conception, initiation, and control of action. We have already seen that the SMA is involved in the organization of motor sequences based on plans, and that PM is involved in the preparation of a specific action. But that is not all there is to it: the prefrontal cortex is involved in the initiation and in the temporal organization of action (as described in Chapter 7), and the cerebellum is involved in the temporal control of action sequences. All these regions show anticipatory activity in relation to a forthcoming action. In fact, connections from one area to another typically are mirrored by feedback connections from the “receiving” area to the “sending” one; information is running in both directions, which presumably allows the areas to coordinate their processing.

In short, motor cognition relies on a multicomponent system, with many distinct processes that occur simultaneously, and these processes occur in different brain regions that support different neural networks.

1.3. The Role of Shared Representations

In the realm of motor cognition, the concept of **shared motor representations** refers to our ability mentally to represent actions made by other people. As we shall see, the same kinds of motor representations are formed when we observe someone else act as when we ourselves perform the same action. Thus, by observing, we can acquire representations that later allow us to think about actions. These shared representations are critical in motor cognition because they allow us to learn by observing the experiences of others (just as we can learn affective reactions by observing others, as discussed in Chapter 8). The notion of shared representations is widely used in social psychology, especially in the field of communication. For a successful conversation to take place, speaker and listener have to ascribe similar meanings to words and must have the same concept of the topic of communication (Krauss & Fussell, 1991). When you say “What I mean by that is . . .” you’re making sure that the representation you hold is in fact shared by your listener, so that your responses “make sense” to both of you and advance the conversation. Such shared representations of the meaning of words and social interactions become internalized, that is, represented so that they can be used in mental processing even in the absence of an on-going social interaction. In the same way that shared linguistic representations enable a conversation, shared motor representations make it possible for us to interpret the meaning of the actions of others and respond appropriately. Shared motor representations were presumably elaborated early in our evolution by interactions with the physical and social environment.

As with your response to Watson's encounter with the hound of the Baskervilles, your ability to identify with the protagonist relies in part on the physical and motor responses that the character's behavior triggers in you, the reader.

✓ Comprehension Check:

1. What is motor cognition?
2. What are the major motor areas of the brain and what sorts of functions do they support?

2. MENTAL SIMULATION AND THE MOTOR SYSTEM

The moment Holmes emptied his gun was the final stage of a set of processes by which his action was planned in response to the dramatic event he witnessed. Do you think his reasoning processes relied on the kinds of logical deductions and inductions we discussed in Chapter 10? In fact, there is evidence that a different sort of cognition underlies our reasoning in action situations. Specifically, one way we reason is by forming and transforming mental images of possible actions, and “observing” the consequences of those actions. This makes sense because imagery and perception share most of the same neural mechanisms (Ganis et al., 2004; Kosslyn et al., 1997; Kosslyn et al., 2006). Thus, “watching” the events in a mental image can change our behavior, much as can watching another person's behavior. Indeed, many athletes believe that mentally rehearsing their movements before executing them on the field helps them to perform better, and research supports this belief. It has been demonstrated that **motor imagery**—mentally simulating an intended action without actually producing it—has a positive effect on subsequently performing that action (Feltz & Landers, 1983).

Not only can motor imagery guide our motor cognition, but our motor cognition in turn can affect our motor imagery. Converging evidence from several sources indicates that motor imagery involves processes involved in programming and preparation of actual actions. The essential difference is that in the case of motor imagery, the action is not performed. Still, the processes underlying motor cognition can direct the way mental images are transformed. In this section, you will see that the mechanisms that allow us to produce actions also allow us to anticipate the likely consequences of performing an action.

2.1. Motor Priming and Mental Representation

Mental simulations must be guided by specific types of mental representations. We gain insight into the nature of such representations by considering a type of priming. Priming, as we've discussed before, is the facilitation of processing that results from performing a previous process. In the investigation of motor cognition, **motor priming** is the effect whereby watching a movement or an action facilitates making a similar motor response oneself. Motor priming provides evidence for shared

representations when we observe a movement or an action and when we produce the corresponding movement or action ourselves. The existence of these shared representations suggests that mental simulations are particularly useful for reasoning about possible actions that you or someone else could take. Consider the results of three studies that have explored perception–action cycles.

To examine the effect of perception on motor production, investigators designed an experiment based on reproducing observed motion (Kerzel et al., 2000). Participants were instructed to watch a “launching event” on a computer screen in which a disk (object A) collided with another disk (object B) and appeared to set object B into motion. The researchers varied the velocity of both object A and object B. Immediately after watching a launching event, participants were asked to reproduce the velocity of object A by moving a stylus from left to right on a tablet. The researchers found that not only did the perceived speed of object A influence participants’ reproduced velocities but, even though participants had been asked to reproduce *only* the speed of object A, their velocity reproductions were also influenced by the speed of object B. Simply having perceived object B primed the participants, influencing the speed at which they later moved object A.

A more complex task, which echoes the Stroop effect, was required of participants in a study that investigated the relationship between perception of another person’s movements and production of movement oneself. The investigators presented participants with views of two manual gestures, hand spreading and hand grasping (Sturmer et al., 2000), as shown in Figure 11–2. Participants were instructed to spread or clench their own hands according to the *color*, not the position, of the stimulus hand: red meant “grasping,” blue meant “spread.” The researchers observed that the speed of the response was quicker when the position of the stimulus hand matched the required response—for example, grasping when the stimulus hand was red *and* grasping; the grasping response was slower if the stimulus hand was red and spread. The perception of the stimulus hand position—although irrelevant to the

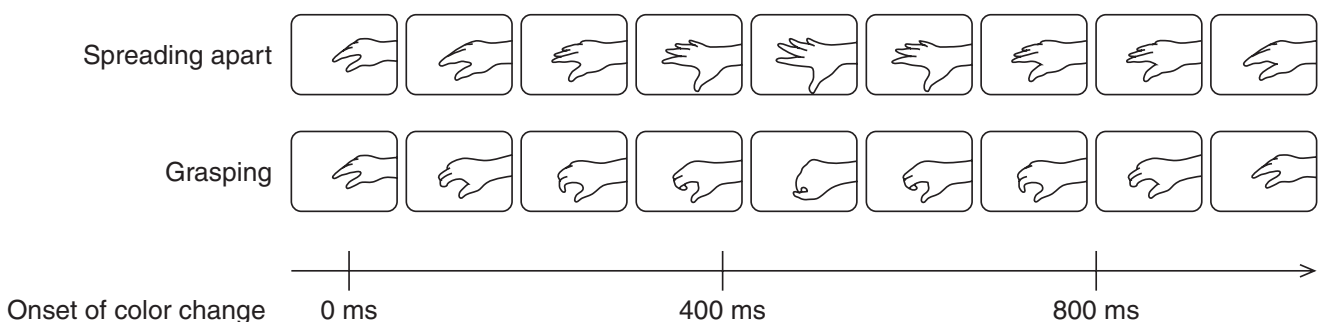


FIGURE 11–2 Hand position research

Sturmer, Aschersleben, and Prinz (2000) showed participants these hand positions. The color changed to red or blue, which cued the participants to grasp or to spread their own hand. The participants responded more quickly when the position of the stimulus hand matched the required response.

(Sturmer, B., Aschersleben, G. & Prinz, W. (2000). Correspondence effects with manual gestures and postures: A study of imitation. *Journal of Experimental Psychology: Human Perception and Performance*, 26, 1746–1759.)

task—clearly influenced the production of the movement itself. We cannot ignore the actions of others, and these actions prime corresponding actions in ourselves.

In addition, Castiello and colleagues (2002) explored the nature and specificity of motor priming by studying behavioral responses to actions by a robotic arm and by a human arm. Consistent with the conclusions we drew in the previous section, in four separate experiments these researchers found a priming advantage for a human arm over a robot arm—that is, the participants' responses were faster when the model was human. The human model also produced more specific and subtle responses in the participants than did the robot model: for example, viewing a human model led participants to adjust the width of their grasp depending on the grasp of the observed model, but no such effect occurred when participants watched a robot model.

Taken together, the findings in these investigations suggest that simply observing a movement or an action can prime a similar response in the observer. These results provide support for the inference that observing a movement or an action and performing the corresponding action share a representational system. These representations can be triggered in many different ways, including by reading the words of a master storyteller. Now it is less of a surprise that your body responded to Watson's dreadful experience when you read *The Hound of the Baskervilles*.

2.2. Motor Programs

You're at the wheel of a car, waiting at a traffic signal for the light to turn green. If you anticipate the signal change, you will be quicker to respond to the light when it turns green. This is because when you anticipate, you (sometimes unconsciously) set up a **motor program**, the representation of a sequence of movements that is planned in advance of actual performance, necessary to accomplish releasing the brakes and stepping on the gas pedal. Motor programs underlie motor cognition; you can run them not only to produce a movement, but also to reason about the consequences of moving in specific ways.

Studies of response time (RT) have contributed extensively to the investigation of motor programs. One way to study the nature of motor programs is to observe what happens right before a person must perform an action. In the framework of information-processing models, the concept of **motor anticipation** refers to the set of processing operations required to prepare a motor program. Such processing occurs after the stimulus is identified and before the response is executed. During the first part of the preparation process, the electrical activity that would be recorded when a muscle is contracted is silent, whereas later in the process, the muscle is activated before the movement begins. This contrast is strong evidence in favor of mental processes being used to set up motor programs. Such findings demonstrate that there are two distinct stages to motor anticipation: the planning processes—which can also be used to create mental simulations—and the processes that initiate production of the response. Furthermore, it has been demonstrated that the time to begin a response after a cue increases with the complexity of the action, a relationship that suggests that a more complex action requires more time to plan.

What exactly is happening in the brain during motor anticipation? In humans, brain electrical activity can be measured by electroencephalography (EEG). Electrical negativity is related to cortical activity, and it is well known that before a movement there is a slow buildup of such an electrical signal over the central regions of the cortex. This electrical signal, called the *readiness potential*, appears to originate in the SMA. Another such signal, originating from the prefrontal cortex, precedes voluntary action by a longer time than does the readiness potential. In addition, fMRI studies have demonstrated that anticipation is not restricted to an increase in activation in the SMA, but also includes the parietal cortex, the thalamus, and the cerebellum (Decety et al., 1992). These findings suggest that motor anticipation takes into account not only the desired movement itself (the output of the system), but also its context and means. Such representations could be useful not simply to control movements, but also in many forms of reasoning and problem solving.

As we mentioned earlier, to use motor representations in reasoning and problem solving, you need to prevent yourself from actually moving (at least until you are ready). Motor anticipation has inhibitory effects at the spinal level, the level of reflexes that—to be useful—must take place very quickly, in less time than would be necessary for the stimulus to reach the brain for processing and response. It has been demonstrated that during preparation for a movement, inhibition occurs at the level of the vertebra corresponding to the relevant set of muscles. Preparing to kick a soccer ball, for example, would involve inhibition relatively far down the spinal cord, whereas preparing to throw a baseball would involve inhibition farther up. This mechanism allows the blocking of the movement by massive inhibition acting at the spinal level to protect motor neurons against a premature triggering of action. It is this inhibitory mechanism that enables you to keep from dropping a hot cup of boiling water when the water sloshes over onto your hand.

Here's an interesting twist, which provides insight into how motor cognition can be used for more than reasoning about our own actions: the representations that underlie our own motor programs are also used to anticipate the actions of others. This was demonstrated by a neuroimaging study in which participants were shown a black dot on a screen, moving as if someone were hand-writing a letter or, alternatively, as if someone were beginning to point to either a large or a small target (Chaminade et al., 2001). In both conditions perception of the first part of the movement of the dot influenced participants' expectation of the next. For example, seeing a dot move as if someone were hand-writing produced activation in cortical areas used to produce hand-writing. By the same token, studies have shown that people can visually anticipate the consequence or outcomes of actions. Flanagan and Johansson (2003) investigated participants' eye movements while they watched another individual perform a task. The observers' eye movements were similar to those that occurred when participants actually performed the task.

We have been discussing motor programs largely in the context of guiding ongoing actions, but we humans can also use such programs to anticipate and plan our future actions. One way to do that is by imaging how we would behave in various contexts.

2.3. Mental Simulation of Action

It is now a small step to see how we can set up “mental simulations” of actions. We build the same motor programs that could control action, but stop them from engaging the neural structures that actually produce movements. Instead, we use the motor programs to guide movements in mental images, which allows us to “see” the consequences of certain actions. For example, you can note the precise angle at which you should hold your hand in order to shoot one of that giant hound’s vital organs. Unlike the situation with motor programs, we are aware of our mental simulations.

If the same motor programs that guide movements in mental images also guide actual movements, then we would expect that practicing with mental imagery should help a person learn to perform the corresponding activity. And, in fact, much behavioral and neurophysiological evidence has shown that motor imagery has significant positive effects on motor skill learning, that is, on the mastery of a complex action sequence such as putting a golf ball. Indeed, researchers have demonstrated that changes in motor programs induced by mental training may actually make a person stronger. For example, Yue and Cole (1992) compared finger strength in two groups, one that performed repeated isometric muscle contractions and one that received motor imagery training alone, learning to imagine making the movements without actually making them. Both groups increased finger strength, the isometric contraction group by 30 percent, the imagery group by 22 percent. Thus, strength increases can be achieved without repeated muscle activation.

One reason why motor imagery allows us to plan actual actions is that the constraints of the physical world shape our imagery in a manner similar to how they shape our actions. For example, when participants are asked to mentally walk toward targets placed at different distances, the amount of time it takes to perform this task varies according to the distance of the target. Moreover, the time it takes participants actually to walk toward the target is highly correlated with the time it takes them to imagine doing so. And when asked to imagine themselves walking toward a target while carrying a heavy load, participants reported longer times to reach the target than when asked to imagine walking the same distance while carrying a light load (Decety, 1996). In addition, Parkinson’s patients (who experience a slowing of movements), when asked to produce and to imagine sequential finger movements, are slowed at *both* tasks (Dominey et al., 1995). Taken together, these findings suggest that motor imagery and motor production exploit the same representations and that the physical characteristics of objects and events exert an influence on both imagined and performed actions.

The neural difference between motor performance and motor imagery performance seems essentially to be a matter not of “what” but of “how much.” The motor regions in the brain are activated not only during actual performance, but also in imagery, but less strongly than during actual performance. An fMRI study in which participants were requested to actually or mentally execute a finger–thumb opposition task found that the contralateral motor cortex was activated in both tasks (the imagery results are shown in Figure 11–3). In the mental execution task, however, the activation was never more than 30 percent of that found during actual execution (Roth et al., 1996).

Running across a dark moor to rescue a friend from the attack of a monstrous dog—as Watson is doing in the lines from *The Hound of the Baskervilles* quoted

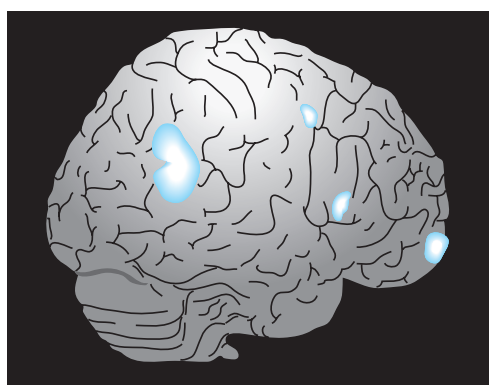


FIGURE 11–3 The power of motor imagery

Actually performing and consciously imagining an action—in this case, repeatedly touching thumb and finger—recruit similar sets of cortical areas: the premotor, motor, and parietal cortex and the cerebellum. (Roth, M., Decety, J., Raybaudi, M., Massarelli, R., Delon, C., Segebarth, C., Morand, S., Decorps, M. & Jeannerod, M. (1996). Possible involvement of primary motor cortex in mentally stimulated movement: an fMRI study. *NeuroReport*, 7: 1280–1284. Reprinted by permission of Lippincott, Williams & Wilkins.)

at the beginning of this chapter—is a pretty dramatic situation, and the anecdotal evidence of many readers of thrillers suggests that a character’s hard breathing and elevated heart rate can be mirrored in readers’ responses. To find specific evidence for this kind of relationship, researchers investigated (in less hazardous circumstances) the idea that mental simulation taps the same neural processing as does actual experience, as reflected at the level of autonomic functions such as heartbeat and respiration (not generally under voluntary control). In a study that has been replicated by several research groups, measurements of cardiac and respiratory activity were made in healthy volunteers asked to perform a treadmill exercise at speeds of 5, 8, and 10 kilometers per hour (Decety et al., 1991). They were also asked to mentally simulate walking or running on the treadmill, coordinating their effort to the noise of the treadmill recorded during the actual exercise session. Both heart rate and pulmonary ventilation varied with the degree of imagined effort, although not to the point of equivalence with the physical exercise. The degree of actual autonomic activation of a participant mentally running at 12 kilometers per hour was comparable to that of a participant actually walking at 5 kilometers per hour. Nevertheless, imagery alone changed heart rate and breathing rate, which is powerful evidence that imagery can engage the autonomic nervous system.

What is the relationship between imagining your own actions via a mental simulation and anticipating seeing someone else’s actions? To investigate this issue, Ruby and Decety (2001) asked volunteers either to imagine specific familiar actions such as brushing their teeth or stapling papers, or to imagine another person doing the same things. For a more detailed look at this work, see the accompanying *A Closer Look* box. The results indicated that both imagining themselves and imagining others performing a given action produced activity in the premotor cortex, the SMA, and the precuneus. These regions of the brain may account for shared motor representations between self and other. However, the overlap is not complete. When participants imagined their own actions, there were specific activations in the inferior parietal and

A CLOSER LOOK

Taking Perspective

Perrine Ruby and Jean Decety investigated the neural underpinnings of the phenomenon of taking another's perspective, that is, imagining someone else performing an action. They reported their results in 2001 in a paper entitled "Effect of Subjective Perspective Taking during Simulation of Action: A PET Investigation of Agency," *Nature Neuroscience*, 4, 546–550.

Introduction

Researchers have demonstrated a striking similarity between the neural networks involved in producing an action and in imagining oneself performing this action. This network includes, in right-handed people, the inferior parietal and premotor cortex, the supplementary motor area (SMA) on the left side, and the right cerebellum. The present investigators asked "What processes are engaged when we imagine not ourselves acting, but rather someone else acting?"

Method

The investigators scanned the brains of individuals while they mentally simulated various everyday, familiar actions (for example, winding a watch); the participants were asked to simulate these actions either from their own perspective (imagining themselves performing those actions) or by adopting the perspective of observing another person (imagining the other person performing those actions). All actions selected for the study required the use of the right dominant hand. The participants (right-handed) were trained in the tasks before neuroimaging. In the scanner, these two perspectives were initiated either from photographs of familiar objects or from sentences describing familiar actions. Two baseline conditions were also performed (photos and spoken sentences). Each stimulus was presented for 5 seconds.

Results

Both the self-perspective and other-perspective mental imagery conditions evoked common activation in the SMA, premotor cortex, and the occipitotemporal region. However, the overlap between the two conditions was not complete. Adopting the perspective of another individual to simulate his or her actions resulted in selective activation of the frontopolar cortex and right inferior portion of the parietal lobe.

Discussion

This study demonstrates that imagining oneself acting and imagining another individual acting involve common neural resources. This finding is compatible with the idea that the same neural code is used in action production, imagination, and perception (Decety & Sommerville, 2003). The researchers also propose that the specific activation of both right inferior parietal cortex and frontopolar cortex when imagining the other acting provides a means whereby we can determine agency—whether an action should be attributed to ourselves or to another agent.

somatosensory cortices in the left hemisphere. When participants imagined the actions made by another person, additional activations were detected in the right inferior parietal lobule, the posterior cingulate, and the frontopolar cortex. These regions play a role in *distinguishing* the self from the other within the shared neural motor representation.

Finally, you might wonder whether *all* mental simulations rely on motor cognition. The answer is no. First, consider a classic finding reported by Shepard and Metzler (1971), illustrated in Figure 11–4. In this task, participants are asked whether the two objects in each pair are identical or are mirror images (try it yourself). Participants report that they “mentally rotate” one object until it lines up with the other, and only after this *mental rotation* do they compare the two objects. And, in fact, the further the object on the right needed to be rotated to line up with the one on the left, the longer the participants required to answer the question. The findings indicate that people not only can rotate objects in two dimensions, as if watching a CD spin, but also can do so in depth.

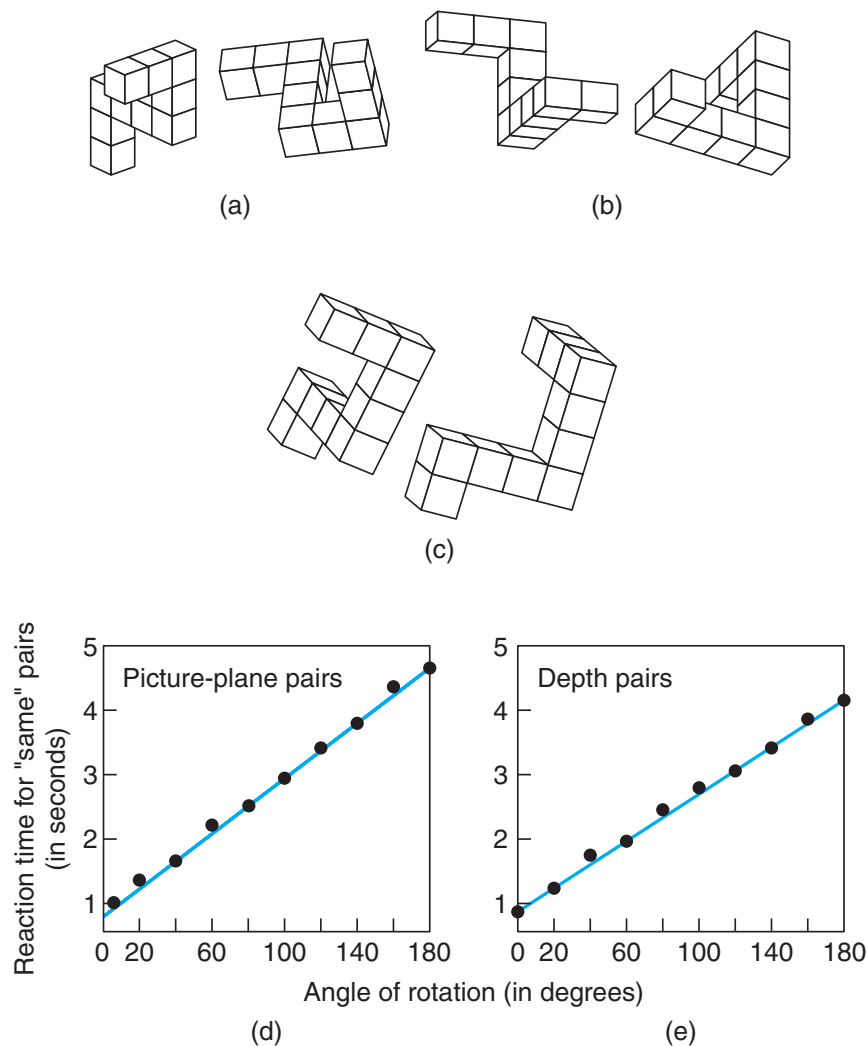


FIGURE 11–4 Mental rotation

When deciding whether the objects in each pair are identical or are mirror images, participants report mentally rotating one until it lines up with the other. And, in fact, the more rotation that is necessary, the more time the participants require (as shown in the graphs). This occurs both with picture-plane rotations (which occur in only two dimensions, such as occurs when a CD is spun around on a table-top) and depth rotations (which occur in the third dimension).

(From “Mental Rotation of Three-Dimensional Objects,” by R. N. Shepard and J. Metzler, 1971, *Science*, 171, pp. 701–703. Reprinted with permission.)

How is such mental rotation accomplished? Research findings have shown that there is more than one way we can perform this task. For example, Kosslyn and colleagues (2001) asked participants to perform the Shepard and Metzler task while their brains were being scanned, and gave them specific instructions about how to imagine the objects rotating. In one condition, the participants were asked to imagine physically rotating objects (by twisting them in their hands). In this case, the primary motor cortex and other motor areas were activated—which is good evidence that motor cognition was at work. In the other condition, the participants were asked to imagine that an electric motor rotated the objects. In this case, the motor areas of the brain were not activated (but other frontal and parietal areas were)—which speaks against the involvement of motor cognition.

Many additional research findings have converged to show that although some types of mental simulations are guided by motor information, other types are guided by perceptual information about how objects appear when they move or interact in specific ways (Stevens, 2005). As we discussed in Chapter 4, mental simulations may be grounded in perceptual representations. Nevertheless, there is considerable evidence that motor cognition can also guide our mental simulations (which is why the two types of simulations are presented in the same chapter of this book).

✓ Comprehension Check:

1. What does motor priming tell us about motor cognition?
2. What is a motor program, and how are motor programs used in cognition?

3. IMITATION

How do we know which movements will achieve a certain goal? Without such knowledge, mental simulations could not operate. A fundamental idea is that we acquire such information partly by observing others. In fact, our cognitive systems are tailor-made to allow us to acquire knowledge of the consequences of actions by observing other people.

Specifically, we benefit from observing others and imitating them. Unlike **mimicry**, which is the tendency to adopt the behaviors, postures, or mannerisms of others without awareness or intent (Chartrand & Bargh, 1999), **imitation** is the ability to understand the intent of an observed action and then to reproduce it. Mimicry is highly present in nature; imitation is largely restricted to humans. This immensely useful attribute is even acknowledged to play an important role in cultural learning (Tomasello, 1999).

3.1. The Development of Imitation

The ability to imitate has been of interest to developmental psychologists for many decades. Initially, researchers thought that imitation was a sophisticated and late-developing ability. The famous developmental psychologist Jean Piaget (1953)



FIGURE 11–5 The power of imitation

Even newborns can imitate facial expressions.

(From “Imitation of Facial and Manual Gestures by Human Neonates,” by A. N. Meltzoff and M. K. Moore, 1977, *Science*, 198, pp. 75–78. Reprinted with permission.)

claimed that infants’ capacity to imitate does not emerge until approximately 8 to 12 months of age. Younger infants were thought to lack the ability to match observed movements with their own internally generated movements.

Studies during the last three decades have challenged this view. In a landmark study, Meltzoff and Moore (1977) demonstrated that imitation occurs even in newborn infants. Newborns shown simple facial gestures such as lip protrusion, mouth opening, and tongue protrusion are able to reproduce these gestures (Figure 11–5). Moreover, imitation is observed even after a delay is introduced between the stimulus and the response, ruling out reflexes as an account for the infants’ reflection of the gesture.

Whereas initially infants imitate actions that are bodily directed, such as sticking out their tongues, by 6 months of age they can also imitate actions on objects, such as shaking a rattle (Butterworth, 1999). In addition, with age infants develop the ability to engage in deferred imitation over increasingly longer periods of time

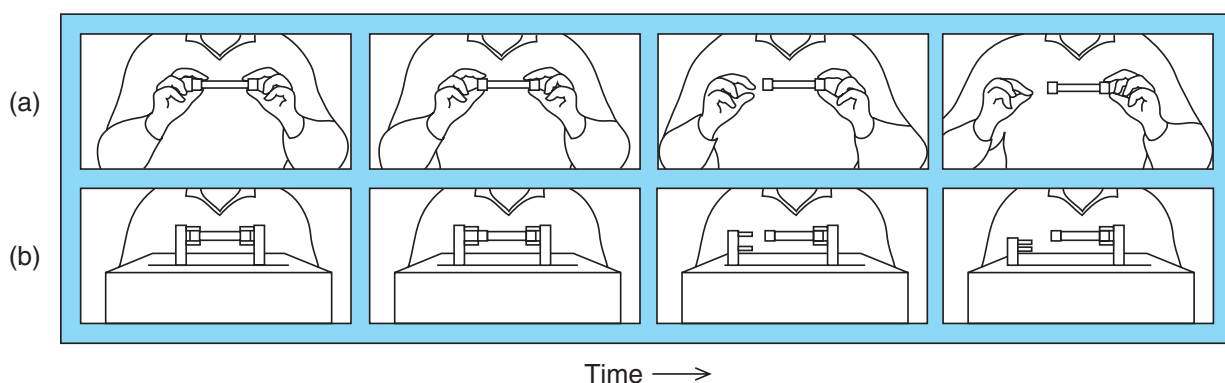


FIGURE 11-6 What—or whom—do we imitate?

Eighteen-month-old children watched either (a) a human actor or (b) a mechanical device attempting to pull apart a dumbbell. All the children watched with interest, but only the children who watched the human actor imitated the action.

(Andrew N. Meltzoff, *Understanding the Intentions of Others: Re-Enactment of Intended Acts by 18-month-old children*. *Developmental Psychology*, 1995, vol. 31, no. 5, fig. 2, p. 844. Copyright © 1995 American Psychological Association. Reprinted by permission.)

(Barr et al., 1996). Moreover, even early imitation is not restricted to bodily movements but also includes facial emotional expressions (e.g., Field et al., 1982).

Meltzoff and Gopnik (1993) argued that infants' imitation of emotional facial expressions creates an internal feeling state in the infant that matches the partner's feeling state. A compelling demonstration of normal infants' self–other connection is illustrated by studies that show that infants imitate actions of people but not of objects (Legerstee, 1991). This result has been further explored with the reenactment procedure used by Meltzoff (1995), which makes use of toddlers' natural tendency to pick up behavior from adults, reenacting or imitating what they see. For example, in one study, two groups of 18-month-old children were shown either a human demonstrator or a mechanical device, both of them attempting to pull apart a dumbbell (Figure 11-6). The human actor never succeeded; a hand always slipped off one end of the dumbbell. The mechanical device failed in a similar fashion, its pincers sliding off the object. All the children were visually riveted by both displays, but only the children who had watched the human actor tried to dismantle the dumbbell themselves. Children apparently mentally represent the behavior of others in terms of goals and intended acts, instead of purely physical movements or motions. It may also be that children identify more closely with humans than with machines and unconsciously assume that they have competencies similar to those of other humans.

Furthermore, infants imitate what they understand. For example, fifteen-month-olds are happy to imitate an adult putting a bird to bed, but they are less willing to imitate an adult putting a car to bed (Mandler & McDonough, 2000). They not only represent actions as goal directed, but also seem to be able to have beliefs about what constitutes plausible goals.

In sum, these findings provide further evidence that the perception–action cycle is part of our built-in machinery for reasoning and problem solving; even young

infants rely on comparable mental representations for their own and others' actions. Moreover, these findings fit neatly with the idea that we use our action system as a model to understand others's actions, which allows us to acquire motor representations from others, which we then can use to guide our own behavior.

3.2. The Cognitive Components of Imitation

If imitation were simply an automatic response like mimicry, it would not be of much use to us. After all, humans are not parrots. Our needs are far more diverse, and complex imitation is not reducible to mere perception or to a direct connection between perception and action. Instead, imitation includes having a plan to observe and then reproduce the observed movements, achieving the goal of the action, and reproducing the means by which the goal is achieved.

As we have seen in previous chapters, our goals and intentions affect how we process stimuli in the world. In fact a series of neuroimaging studies (Decety et al., 1997; Grèzes et al., 1998, 1999) has demonstrated that the *intention* to imitate actions has a top-down effect on the brain regions involved in the *observation* of actions (Figure 11–7). In these studies, adult participants were instructed to watch carefully actions performed by a human model either for later recognition or for imitation.

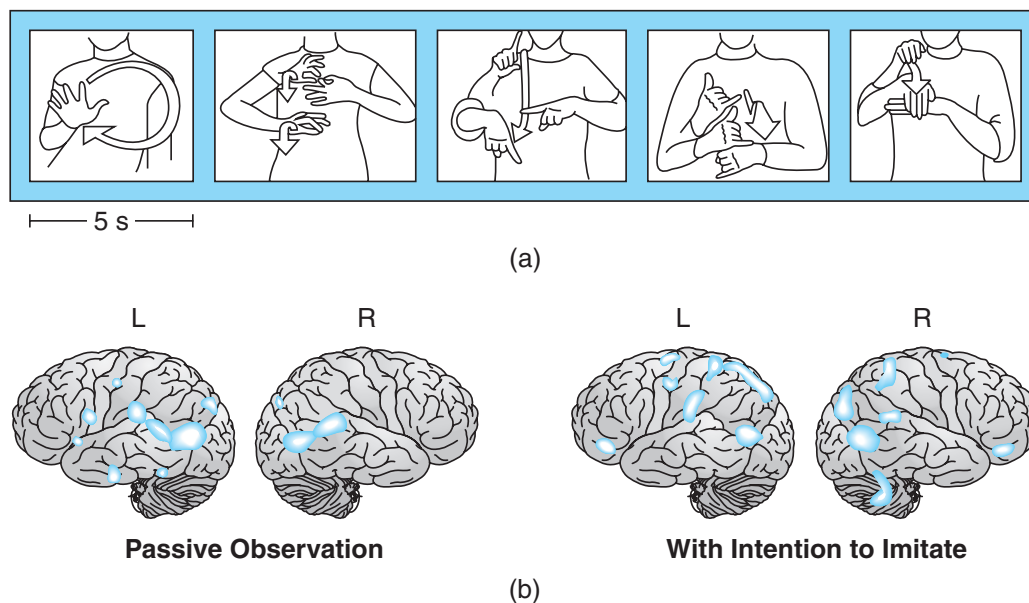


FIGURE 11–7 The power of intention

(a) Participants were shown a human model performing these actions, each for 5 seconds. (b) When they observed the actions for later imitation, as compared with passively observing the same actions, additional brain activation was detected in the supplementary motor area (SMA), the middle frontal gyrus, the premotor cortex, the anterior cingulate gyrus, and superior and inferior parietal cortices in both hemispheres. ("L" and "R" stand for left and right hemispheres.) Thus, the intention to imitate has a top-down effect on the information processing recruited when we observe actions.

(Decety, J., Grèzes, J., Costes, N., Perani, D., Jeannerod, M., Procyk, E., Grassi, F. and Fazio, F. 1997. Brain activity during observation of actions. Influence of action content and subject's strategy. *Brain*, 120, 1763–1777. Reprinted with permission of Oxford University Press.)

When participants observed actions for later imitation, activation was detected in the SMA, the middle frontal gyrus, the premotor cortex, the anterior cingulate, and the superior and inferior parietal cortices in both hemispheres. A different pattern of brain activation was found when participants were passively observing the actions for recognition (in that case, the parahippocampal gyrus in the temporal lobe was the chief region activated). Thus, intention to imitate has a top-down effect on the information processing involved in action observation. Observing another person in order to imitate serves to tune regions involved in action generation. These studies strongly support the view that observing an action with the intention to imitate it involves neural regions similar to those engaged during actual production of the action.

In addition, the mechanisms that allow us to imitate depend on whether we observe meaningful or meaningless actions. Although normal adults and children have the ability to imitate both types of actions, evidence from research with apraxic patients suggests that the reproduction of meaningful and meaningless actions are mediated by different neural systems. **Apraxia** is a neurological disorder that impairs the ability to make voluntary movements, especially in the manipulation of objects. The left hemisphere, which when damaged impairs imitation, is dominant for the control of action and for language in most people, and it is often the case that apraxic patients have language as well as movement dysfunctions. Researchers have observed that in patients with apraxia the ability to imitate meaningful gestures is relatively spared, whereas the imitation of meaningless gestures is impaired (Goldenberg & Hagmann, 1997). On the basis of clinical observations, Rothi and colleagues (1991) postulated the existence of at least two partially independent processing routes. One route passes via long-term memory representations of familiar (and therefore meaningful) gestures. The other route, which can be used for the imitation of both meaningful and meaningless gestures, provides a direct link from perception to movement production.

Studies with normal participants showed that they too are better at imitating meaningful actions than meaningless ones: they were able to hold more meaningful than meaningless actions in working memory (Rumiati & Tessari, 2002). Also in normal participants, different brain regions are activated in imitation of the two types of action. In fact, different brain regions are involved when participants merely observe the two kinds of actions. For example, a PET study of participants observing meaningful actions showed strong engagement of the left hemisphere in frontal and temporal regions, whereas observation of meaningless actions involved mainly the right occipitoparietal pathway (Decety et al., 1997). These results support the view that meaningless and meaningful actions are processed via different routes.

What is acquired when we imitate? Not just the behaviors themselves. Rather we acquire the means to generate a motor program to achieve a goal. Humans have the ability to reproduce the goal state of an action (such as picking up a coffee cup), even when it requires reaching in a different way from what was observed, and to vary the means of achieving the goal (such as sliding—ever so carefully—a napkin on which the cup rests in order to bring the cup within reach before picking it up); and we can do this even in the absence of the model we initially observed (Tomasello, 1999). In one study, 14-month-old infants saw an event in which a human actor activated a light panel using her head, not her hand. When the reason the actor did not

use a hand to manipulate the light panel was clear (if, for example, she was holding a blanket around her body with both hands), the toddlers imitated only the goal of the event, turning on the light panel by any available means. In contrast, when it was not apparent why the actor used her head to turn on the light, the toddlers reenacted both the means and the goal, using the head as did the model (Gergely et al., 2002).

Chaminade and colleagues (2002) used neuroimaging to attempt to identify to what extent, if any, the neural processing of goal and means differs. (In the language used in the problem-solving chapter, it's the difference between a "goal state" and a series of "operators".) In this experiment participants saw a human model making Lego constructions. The goal was defined as placing a block in a specified position and the means was defined as the motor program—the specific series of movements—used to achieve the goal. Participants were shown either the means and the goal (the whole action performed by the model, ending with block in position); the goal only (the block in the specified position); or the means only (the sequence of movements). All the participants were asked to imitate what they observed. When participants imitated either the goal or the means, there were partially overlapping clusters of activation in the right dorsolateral prefrontal cortex and in the cerebellum. This implies that these regions are involved in processing both the goals and the means of the action with the intention to imitate. Moreover, specific activity was detected in the medial prefrontal cortex during the imitation of the means, whereas imitating the goal was associated with increased activity in the left premotor cortex. Clearly, the processing of means and of goals is not identical. The act of imitation appears to involve two components (means and goals) that are at least partially dissociable.

Interestingly, an activation of the right medial prefrontal region was found only in the imitation of the means (Figure 11–8 on Color Insert O). This region is known to play a critical role in inferring others' intentions, and is consistently involved in tasks that require an understanding of the mental states of others (Blakemore & Decety, 2001). Its activation during imitation supports the idea that imitation involves inferring or identifying the intention of an action.

3.3. Simulation Theories of Action Understanding

Imagine yourself as Holmes. Seeing your friend attacked, you would probably have the same intention and consequently generate an action plan similar to Holmes's—disable the beast as fast as you can. When we put ourselves in another's place, either by observation or pure imagination, we can understand their plans (and later use such plans ourselves). How is it that we can come to understand the plans of others, if we must take into account unobservable, private, internal mental states?

Considerable speculation has surrounded this question for centuries (see the accompanying *Debate* box). Many researchers have speculated that our own actions, and their accompanying mental states, serve as a rich source of information for understanding the actions of others. In modern times, at least as far back as James Mark Baldwin (1861–1934), an early leading figure in experimental psychology, theorists have suggested that our experience as agents helps us to understand others

How Do We Know Whose Plan It Is?

DEBATE

The evidence indicates that we represent others' plans for actions in much the same way as we represent our own. Taken at face value, evidence for a shared representational system for actions of the self and actions of the other implies a paradox: if representations are in fact shared, how can a distinction between self and others be preserved? At first glance the answer may seem straightforward: we have a representation of the "self" and know when that representation is associated with plans. However, speculation on the nature—indeed, on the very existence—of the self is an age-old question. Perspectives have ranged from viewing the self as a tangible unified mental entity (Descartes, 1641/1985), to seeing the self as an illusion arising from various perceptions and sensations (Hume, 1739; James, 1890), to seeing the self as a mythical entity (Kenny, 1988). Twenty-first-century research findings can shed light on this classic debate.

Certainly it is true that sometimes we misreport actions performed by another as performed by the self and vice versa (Frith et al., 2000). Nevertheless, neuroimaging experiments have failed to find a "self center" in the brain (although there is some evidence for a role of the right prefrontal cortex in self-processing; see Keenan et al., 2000); instead, they have identified a set of areas, including the inferior parietal cortex, the insula, the posterior cingulate, and the prefrontal cortex, that—among other roles—play a role in the distinction between one's own action versus actions performed by others (Blakemore et al., 1998; Decety et al., 2002; Farrer & Frith, 2002; Farrer et al., 2003; Ruby & Decety, 2001). We all are usually readily able to attribute an action to its proper agent, we all have a "sense of ownership," and we all have the subjective experience of a sense of self. How is this accomplished?

There is accumulating evidence that the brain contains internal "models" that represent aspects of one's own body and its interaction with the environment (e.g., Frith et al., 2000). This interaction can be described by a feed-forward model of the general sort summarized by Decety and Sommerville (2003), which enables us to recognize the sensory consequences of self-generated actions. Every time a motor command is issued to make a movement, a copy of the motor command, known as an *effference copy*, is produced. This *effference copy* is then used to predict the sensory consequences of that movement (Greenwald, 1970). This sensory prediction is then compared with the actual sensory consequences of the act and the results of the comparison are used to determine the source of sensory events. This is why you cannot successfully tickle yourself: the sensory consequences of that action are predicted and cancelled. The sensory predictions associated with a wide variety of motor actions can be stored, providing a bank on which to draw.

This kind of model has been proposed to account for our awareness of ourselves as the source of our thoughts, desires, and beliefs (e.g., Frith, 1992). Investigators have explored how this feed-forward model could be used to predict what another person will do (Blakemore & Decety, 2001). When you see someone else perform an action, the forward model is reversed. You recruit the sensory consequences of the other person's action from your own model, use them to "estimate" what your own intentions would have been for that action, and attribute those intentions to the other person. The parietal cortex and the insula play a pivotal role in the comparison between one's own and another's intentions.

However, an alternative explanation for distinguishing self versus other within the shared representation network hinges on the timing of activation in a number of cortical areas, with no use of an *effference copy*. Grèzes et al. (2004) showed participants videoclips of themselves and of other, unfamiliar people lifting boxes of different weights. They asked the participants to decide whether the actor they watched had a correct or false expectation of the weight. When participants made this judgment, action-related structures in the frontal and parietal lobes were activated. But more than this, the neural activity started earlier when participants made judgments about their own actions than when they made judgments about

(continued)

others. This latter finding shows that the dynamics of neural activation within the shared cortical network provide a way to distinguish one's own actions from the actions of others. But they do not show that this is all there is to it. Only after future research is conducted will we come to understand exactly how we know when a plan is ours and ours alone, or whether it is in fact being evoked by our understanding of what another person is doing or intending to do.

as agents as well. Baldwin himself believed that imitation was the means by which children come to understand others:

Now as he proceeds with these imitations of others, he finds himself gradually understanding the others, by coming, through doing the same actions with them, to discover what they are feeling, what their motives are, what the laws of their behavior. (Baldwin, 1897, p. 88)

In the early twentieth century, the social theorists Charles Horton Cooley and George Herbert Mead shared the notion that our understanding of other persons is based on analogy to the self. This idea has been taken up by philosophers of mind and psychologists in the form of *simulation theory*, which posits that we gain insight into the plans, beliefs, and desires that motivate others' actions by covertly simulating those same actions in ourselves, without actually performing them (e.g., Goldman, 2002; Gordon, 1986; Harris, 1989; Heal, 1998). Interestingly, this view is also compatible with the simulation theory in the field of physiology, as developed by Hesslow (2002), which is based on three assumptions about brain function: (1) behavior can be simulated by activating motor structures as is done during an overt action but suppressing the execution of that action; (2) perception can be simulated by internal activation of sensory cortex, without external stimuli; (3) both overt and covert actions can elicit perceptual simulation of their normal consequences—for example, by imagining twisting an object, you can produce a mental image of what you would see if the object were rotating (Kosslyn et al., 2001, 2006).

Proponents of the simulation view suggest that the behavior of others can be understood by simulating the same behavior in oneself and reflecting on the mental or internal states that accompany this simulation. The actions of others can also be predicted in this manner: you can put yourself in someone else's shoes, simulate the presumed mental states of the other person, and then deduce a likely action. Such simulations may help us gain access to knowledge stored in implicit representations, which otherwise would remain inaccessible.

3.4. Mirror Neurons and Self–Other Mapping

Until recently, the speculation that our understanding of the actions of others may be based on an analogy to ourselves had received scant empirical support. As we discussed earlier, plenty of research now suggests a common representation for the perception and production of actions (e.g., Prinz, 1997). Work with adults has documented [perception-to-action transfer](#), which is part of the perception–action cycle: watching

an action facilitates the later ability to plan and perform that action (well after priming effects affect such behavior; e.g., Hecht et al., 2001). Moreover, studies have documented perceptual interference during action planning (e.g., Müssler & Hommel, 1997), an effect that should be expected if action and perception share common representations and these similar representations are confused with one another.

We have seen that research reveals a shared neural basis for the observation and performance of action in both human and nonhuman primates. In addition electrophysiological recordings have shown that specific neurons in the ventral premotor cortex of monkeys discharge during execution of hand and mouth movements. But more than this, the same researchers discovered that most of these neurons discharge not only when the monkeys performed an action, but also when they observed the experimenter making a similar action (Rizzolatti et al., 1996). Neurons that behave this way are called **mirror neurons** (see Chapter 8). A subset of these mirror neurons also responds when the final part of an observed action, crucial in triggering the response, is hidden, and can therefore only be inferred (Umiltà et al., 2001). Mirror neurons may play a central role in bridging what you see to what you can plan to do.

Evidence for mirror neurons in humans comes from various studies using different techniques. The first one, conducted by Fadiga and colleagues (1995), demonstrated with transcranial magnetic stimulation (TMS) that there is an increase in excitability of the motor system during the perception of actions performed by another person. This enhancement is selective: it was reflected by activity only in the muscles that the participants would use for producing the action observed (see also Fadiga et al., 2005). Converging evidence was reported in a study that used EEG as participants watched movies of objects in movement, animals in motion, gymnastic movements executed by a person, and still shots of these same events (Cochin et al., 1999). The results suggested the specific participation of the sensorimotor cortex during the observation of human motion. Magnetoencephalographic recordings have also shown activation of the motor cortex (Area M1) during the observation of action (Hari et al., 1998). These findings provide evidence that self and other actions are similarly coded in the brain. As such, they form the foundation for a system in which we can not only understand the actions of others on the basis of the production of our own actions, but also can then use others' actions as the basis for our own future actions.

Moreover, some researchers have proposed that this shared representational basis for self and other actions may serve as a powerful engine in development (Frye, 1991; Tomasello, 1999). If infants use information from their own actions to understand the actions of others, one might expect infants' ability to understand or interpret an action to be related to their own ability to perform that action. To test this hypothesis, Sommerville and Woodward (2005) examined how 10-month-old infants responded to a simple cloth-pulling sequence, one in which an actor pulled a cloth to retrieve an out-of-reach toy. The researchers were interested in the relation between infants' ability to solve this cloth-pulling sequence in their own behavior and their ability to interpret the cloth-pulling sequence—that is, to identify the goal—when it was performed by another person. The results showed that the infants who were the most successful at generating goal-directed solutions in their own cloth-pulling

behavior were the ones who recognized that the actor's actions on the cloth were in fact directed toward the ultimate goal of the sequence: the toy. In contrast, the infants who infrequently used goal-directed strategies to solve the cloth-pulling sequence in their own behavior appeared to misidentify the goal of the sequence in another person's actions. Follow-up analyses revealed that neither age (a proxy for developmental level) nor information-processing capacity (a proxy for intelligence) could account for the differences in action interpretation between the two groups.

In subsequent studies, it has been demonstrated that by 3.5 months infants detect a goal of another person's action better when the infants are given self-reaching experience (Sommerville et al., 2005). These findings provide support for the idea that plans for action and the perception of the actions of others are intimately connected, that they begin in infancy, and that infants' own developing capacities for action may provide them with important information about the actions of others.

However, we must close this section with a caveat: Just as not all mental simulations rely on motor processes, not all cognition about other people relies on motor processes. Motor cognition cannot reveal every aspect of the complex tangled web of beliefs and desires that motivate human beings—either in ourselves or in others (for a critique, see Jacob & Jeannerod, 2005).

Comprehension Check:



1. What are the two “processing routes” we can use in order to imitate? What are their relations to plans, previously stored or newly acquired?
2. What are mirror neurons and why are they important for understanding motor cognition?

4. BIOLOGICAL MOTION

The role of mirror neurons in imitation suggests that what we perceive is influenced by how we can move. If so, then our motor cognition systems may help us see subtle patterns of motion, specifically those that signal the presence of another living organism that plans and intends to carry out specific actions. This notion relies on the fact that all animals, human and nonhuman, produce unique patterns of motion. These patterns, no matter how distinct from one another, are all different from the motion of inanimate objects, and so are collectively called **biological motion**. As illustrated in the fictional, but possible, opening narrative, the ability to perceive biological motion from minimal visual cues can mean the difference between life and death, and we humans are very good at it.

In this section you will see that we humans are sensitive to biological motion, that we can readily distinguish among various types of motion that are on the surface very similar, and—crucially—that our motor cognition mechanisms are involved when a perceived motion is one that also can be produced. These findings are consistent with our conclusions from the previous section; actions are coded in a common framework for production and perception, both for the self and others.

Thus, we are able to observe others' actions and use that information later, when we ourselves are engaged in motor cognition and mental simulation.

These are the conclusions we will reach in this section. Let's now see why these conclusions are justified.

4.1. The Perception of Biological Motion

Like that of any other animal, our survival depends on the ability to identify, interpret, and predict the actions of other creatures. Perception of others' motion, in particular, plays a major adaptive role, important for our ancestors in distinguishing between prey and predator, friend and foe. To serve this purpose, the ability to detect biological motion must be fast, precise, and automatic.

Much behavioral evidence demonstrates that the human visual system is finely attuned to the perception of biological movements. The Swedish psychologist Gunnar Johansson (1973) developed the "point-light technique," attaching small light sources to the wrists, knees, ankles, shoulders, and heads of actors who were asked to perform various movements, such as walking, dancing, and running, in darkness (all that was visible to an observer were the moving lights). When asked to describe what they saw, participants readily identified human figures in motion and recognized the various types of actions performed by the actors. Several other research groups using this technique confirmed that the **kinematic pattern**—that is, the pattern of motion—that emerges from the moving lights is sufficient to convey a vivid and compelling impression of human movements, although the percept collapses to a jumble of meaningless lights when the point-light actor stands still (Figure 11–9).

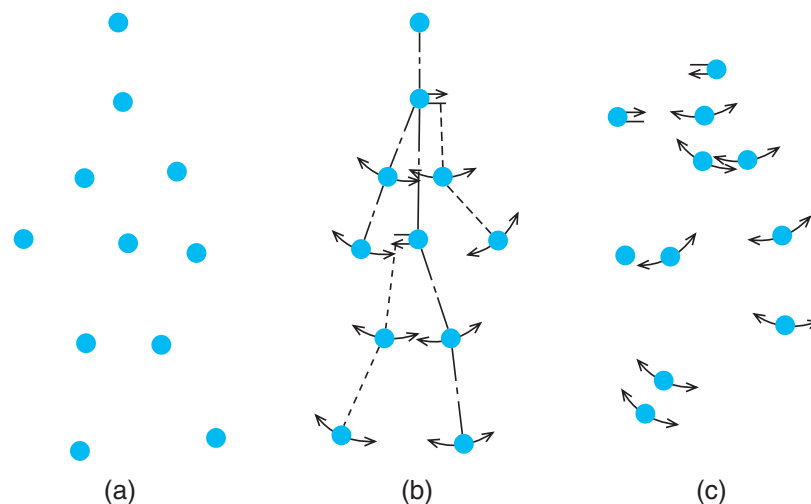


FIGURE 11–9 Our perception of point-light displays

(a) This static display is not usually seen as representing a human form. (b) When the same display moves coherently, it is easily seen as a person walking. (c) If the display moves randomly, it is often perceived as a swarm of bees.

(Bertenthal, B. I. (1993). Perception of biomechanical motion in infants: intrinsic image and knowledge-based constraints. In Carnegie symposium on cognition: visual perception and cognition in infancy. C. Granrud (ed.), pp. 174–214. Mahwah, NJ: Lawrence Erlbaum Associates. Reprinted by permission.)

For example, Kozlowski and Cutting (1977) showed that observers can make very precise discriminations when watching point-light displays, including recognizing the sex of the actors. Even more remarkable, this visual information is sufficient for observers, when filmed themselves as point-light actors, to distinguish themselves from other familiar people. However, when the films were presented upside-down, observers did not report seeing an upside-down human figure. Moreover, our ability to detect and identify biological motion is influenced by the specific kind of action made. Dittrich (1993) showed participants locomotory actions (walking, going upstairs), instrumental actions (hammering, stirring), and social actions (greeting, boxing). Participants recognized locomotory actions more accurately and faster than social and instrumental actions.

Even babies are sensitive to biological motion. Researchers have found that infants as young as 3 months prefer to look at a coherent display of point-lights that is produced by an upright walking person than a display of point-lights produced by an upside-down walking person. This implies that they are detecting the structure of the display (Bertenthal et al., 1984). How is this possible? Several physical constraints allow perception of human biological motion as distinct from object motion. For instance, the wrist can move back and forth and up and down relative to the position of the elbow, but it is always at a fixed distance from the elbow. Bertenthal (1993) proposed that infants' implicit knowledge of such constraints may reflect hard-wired characteristics of the visual system.

The development of infants' ability to detect biological motion provides an intriguing clue to the operation of how we plan our actions. As just noted, infants of 3 months discriminate between an upright and an upside-down point-light walker, as do older babies. But 3-month-old infants also discriminate between an upside-down point-light walker and a random pattern of lights, whereas 5- to 7-month-olds do not. Bertenthal's interpretation of this change is that by 5 months infants are responding to the perceived familiarity of the displays; that is, as a result of experience and accumulated knowledge, they recognize the upright display as a human walker, whereas they perceive the inverted and random displays equivalently because both are alien to their experiences. By the age of 5 months, infants are responding to these sorts of displays at a more complex level of processing as prior knowledge interacts with perception.

Because it seems that observational experience molds infants' developing perception of biological motion, an interesting question is whether the perception of biological motion is limited by an observer's experience of his or her own movement abilities. A fascinating case study is that of A.Z., who was born without limbs (Brugger et al., 2000). A.Z. was asked to judge whether she was viewing a left or a right limb (hand or foot) presented at a range of rotation angles. Normal control participants required more time when they would have to rotate their own limb greater amounts to line it up with the stimulus limb (engaging in a kind of mental rotation). In spite of never having had limbs, A.Z.'s perceptual judgments showed these same physical constraints. Thus, it seems that the perception of biological motion (at least locomotion) does not depend on motor experience per se, and that its core neural mechanism is hardwired.

4.2. Processing Biological Motion

The rapid recognition of a few moving point-lights as depicting the human form suggests that the correct grouping of the point-lights is accomplished by a specific neural network. In fact, researchers have reported a few cases of patients with brain damage who are impaired in the ability to detect biological motion but have few, if any, other deficits (Schenk & Zihl, 1997). The reverse dissociation, where perception of biological motion is intact while other types of perception are impaired, has also been reported (Vaina et al., 1990). The patient in this study suffered an impairment in the ability to discriminate different speeds of motion, and required more than the normal amount of organized information to detect biological motion, and yet had no difficulty in recognizing human activities other than locomotion portrayed by point-light displays.

In addition, Pavlova and colleagues (2003) have examined the visual sensitivity to biological motion in adolescents who were born preterm and had periventricular leukomalacia (PVL). This disorder, a softening of white matter near the ventricles of the brain (possibly caused by insufficient flow of blood to the brain before or at birth), produces early motor disorders. The researchers found in this group that the greater the extent of PVL lesions in the parieto-occipital region, the less the sensitivity to biological motion. These findings suggest that the parieto-occipital region plays a role in the detection of biological motion.

More detailed evidence has come from several neuroimaging (fMRI) studies, which have identified a region in the posterior portion of the superior temporal sulcus (STS) that is active when participants are presented with Johansson-like point-light displays (Figure 11–10 on Color Insert P) (Grèzes et al., 2001; Grossman & Blake, 2001; Howard, 1996). This region lies anterior and superior to the visual area V5 (also called area MT), which is involved in the perception of motion. Another region, in the anterior part of the intraparietal sulcus (part of the parietal lobe) in the left hemisphere, has been found to be engaged during the perception of real human actions (Grafton et al., 1996; Grèzes et al., 1998; Perani et al., 2001). Consistent with our earlier discussion of mental simulation, the mere imagination of biological motion is sufficient to activate the region of the STS, although the activation is weaker than during actual perception of point-light displays (Grossman & Blake, 2001). When you read about the hound jumping onto its intended victim, those words were translated into representations of visual motion—and such representations are processed by cortical areas devoted to processing observed motion.

4.3. Motor Cognition in Motion Perception

When you read about Watson's terrifying experience, you did not confuse his movements with those of the giant hound. Our ability to perceive biological motion goes beyond merely distinguishing the movements of people and animals from those of cars and balls. In one study of children between 29 and 94 months, researchers showed that different cortical areas are involved in perceiving human, animal, and virtual human movements (Martineau & Cochin, 2003). Moreover, neuroimaging experiments have revealed neural activations that are specific to human actions



(a)



(b)

FIGURE 11–11 At the races

(a) *The Derby at Epsom* (1821), by Théodore Géricault. A beautiful painting—and physically impossible. In reality, the moment in a horse's gait when all four legs are off the ground comes not when the legs are extended but when they are collected under the body, as in (b), a photograph of the Preakness winner, 2003.

("The Derby at Epsom," Theodore Gericault (1821). Musee du Louvre, Paris.)

(To come from photo research)

(such as grasping a coffee mug) and that are not elicited by movements with similar visual properties, such as actions in virtual reality displays or actions produced by a robot (Decety et al., 1994; Perani et al., 2001; Tai et al., 2004). Now, let's consider the key question: Why do we perceive motion with such great specificity?

Human movements are the only ones that we produce as well as perceive. Our anatomy places constraints (i.e., limitations) on the actions that we perform, which in turn constrain the way that we can imagine and perceive action—and the way we can imagine actions plays a crucial role in our ability to plan our own actions. Thus, unless we have particular equine knowledge we don't immediately see what's "wrong" in the painting in Figure 11–11. It has been hypothesized that our perception of human movement in others is mediated by *tacit* knowledge of how our bodies work; such knowledge is truly unconscious—we typically do not even know that we have it. And such knowledge plays a key role in guiding our mental simulations—in making them behave in ways that mimic reality.

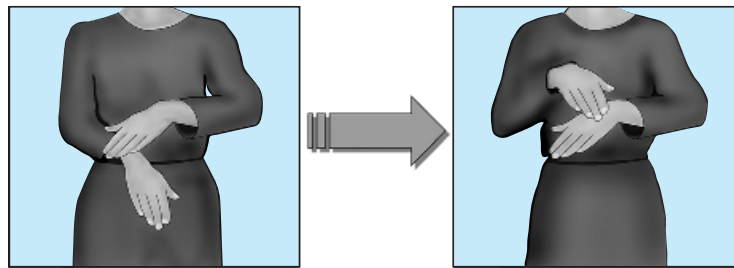
A compelling demonstration of the involvement of tacit motor knowledge in detecting biological movements is provided by studies making use of the phenomenon of **apparent motion**, the illusion created when visual stimuli in nearby locations appear in close succession. Apparent motion is the effect that makes the blinking lights on a theatre marquee seem to be moving around the frame, and the two lights on a construction warning sign appear to be a single light moving back and forth. It's what makes flipbooks and movies possible.

In a series of elegant studies, Shiffrar and Freyd (1990) showed participants alternating series of photographs of a human body in different postures. In one series, the postures were such that the direct transitions between any two sequential photographs corresponded to possible movements. The direct transitions between photographs in the other sequence violated the “solidity constraint” (that one solid object cannot pass through another solid object) and thus were impossible. When participants viewed the two series, the apparent motion they saw between two sequential photographs changed with the amount of time between the presentation of one photograph and the presentation of the next. This time between the onsets of two stimuli is called the *stimulus onset asynchrony*, or SOA. At short SOAs, participants reported seeing the shortest—but impossible—motion path, whereas with increasing SOAs they saw the motion path consistent with human movements (Figure 11–12). Paths of biological actions are more likely to be seen at SOAs that match the time in which the action could actually be performed. In contrast, when participants are shown photographs of inanimate objects, they consistently perceive the same shortest path of apparent motion, regardless of the SOA (Shiffrar & Pinto, 2002).

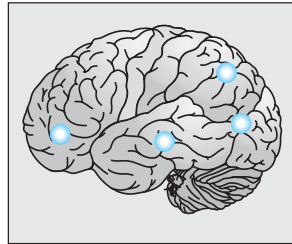
Neuroimaging investigations confirm that differences between perceiving object motion and human motion are due to the fact that there is direct involvement of motor areas in human motion but not in object motion. In one such study participants were presented with static images of a human model in different positions as well as objects in different spatial configurations (Stevens et al., 2000). Members of the pairs were presented in sequence, so that one position seemed to move into the other. The participants were asked to rate the trajectories of the perceived motion path. For the human model, the perceived motion was either a possible or impossible path. The results indicated that the left primary motor cortex, the parietal cortex in both hemispheres, and the cerebellum were activated specifically when participants perceived possible paths of human movement. In contrast, no selective activation of these areas was found during conditions of physically impossible movement paths. Instead, viewing impossible motion paths resulted in a dramatic increase of activity in the ventromedial prefrontal cortex, a region researchers previously found to be involved when people try to comprehend incoherent pairs of sentences (Ferstl & von Cramon, 2002) and social conflicts (Bechara et al., 2000a).

These findings provide evidence that the perception of human apparent motion relies not only on visual processes but also on motor processes, and also that perceiving object motion and human motion rely on different neural networks. Furthermore, the results are consistent with an idea discussed earlier: that we may understand the actions of others in terms of our own motor system and the way that we would plan our own actions (Shiffrar & Pinto, 2002; Viviani, 2002).

But wait a moment—there seems to be a contradiction between the neuroimaging findings using point-light displays and those based on apparent motion. Recognition of human movement in point-light displays is not affected by lesions in the motor production areas, and neuroimaging studies have consistently shown that brain activation is restricted to the temporo-occipito-parietal junction and the inter-parietal sulcus, not motor areas per se. The apparent-motion studies, however, have shown that the perception of biological movements is constrained by the motor

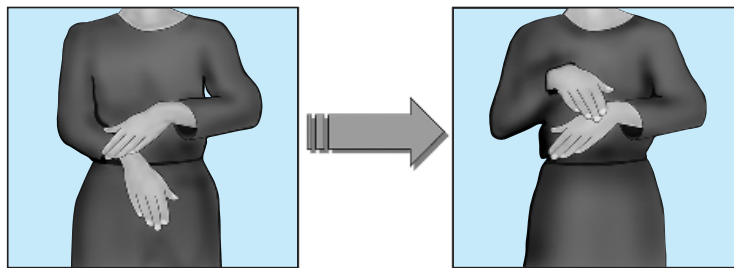


SOA: 150–350 ms

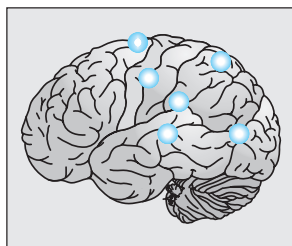


● = Site of activation

(a)



SOA: 550–750 ms



● = Site of activation

(b)

FIGURE 11–12 The phenomenon of apparent motion

(a) A direct path—although physically impossible—is perceived when the interval between presentations of stimuli (the SOA) is short: the hands seem simply to exchange positions. Activation is detected in the frontal lobe, middle temporal gyrus, and posterior parietal lobe. (b) At longer SOAs, an indirect (and possible) path is perceived, one that corresponds to human movements. There is activation in the motor cortex, superior temporal sulcus, and inferior parietal cortex.

(From “The Visual Analysis of Bodily Motion” [pp. 381–399], by M. Shiffrar and J. Pinto, in *Common Mechanisms in Perception and Action*, edited by W. Prinz and B. Hommel, 2002, New York: Oxford University Press. Copyright 2002 by Oxford University Press. Reprinted with permission.)

capacities of the participants, and neuroimaging research has shown that brain areas involved in producing motor actions are activated during visual processing of plausible movements (Grèzes & Decety, 2001; Stevens et al., 2000). How do we account for this apparent conflict?

The explanation for this apparent inconsistency may rest in part on the fact that studies using point-light displays to investigate biological motion often are based on the detection of *locomotion*. Locomotion has a fundamental evolutionary and functional significance and its neural processing is fast and automatic; for those reasons the posterior, superior temporal sulcus alone may be enough to act as a detector, without the involvement of specifically motor areas. On the other hand, studies that investigate apparent motion often use more complex stimuli that, unlike the point-light displays, depict the shape of a human body and the movements depicted are not confined to locomotion. The processing used for these stimuli is thus far more complex than that used for point-light displays.

✓ Comprehension Check:

1. Why is human sensitivity to biological motion relevant for understanding how we reason about actions?
2. What is special about our perception of biological motion?

Revisit and Reflect

1. *What is the nature of motor cognition?*

Motor cognition relies on internal representations that are used to plan and predict our own actions as well as to anticipate and understand the actions of others. As such, these representations are present early in life, elaborated through interactions between the self and others, and can be shared across individuals.

Think Critically

- What is the role of motor cognition in long-term planning (e.g., planning a vacation you'll take in 3 months)?
 - There are constraints on motor cognition and planning that correspond to the way in which the human body is constructed. Research findings suggest, however, that even people with atypical bodies incorporate these constraints in their action perception. If this is the case, what is the role of learning or experience in motor cognition?
2. *What is a mental simulation of action?*

We can create and run motor programs, and “observe” how they affect mental images. We may run such mental simulations in order to achieve a goal, or in an effort to understand another person's actions. In some cases, however, mental simulations are guided not by motor information, but rather by perceptual and conceptual information.

Think Critically

- What sorts of problems are best solved with mental simulations? What sorts of problems are likely to be difficult to solve with mental simulations?
- Does all motor cognition involve mental simulations? (*Hint: We are aware of having mental images—are we aware of all motor cognition?*)

3. *Why and how do we reproduce the actions of others?*

The mental representations used in motor cognition are based in part on our observations of others. The ability to imitate is present very early in life, and plays an important role in understanding others. There is ample evidence to suggest that imitation involves more than simply reproducing observed behavior; rather, we infer others' intentions and goals. When later planning to achieve the same goal, we can use a range of possible actions.

Think Critically

- Does the fact that we humans are capable of imitation imply that we never engage in mimicry? What is the relation between motor priming and mimicry?
- What sorts of plans may not involve actions? Are there any plans that in principle can never lead to actions?

4. *What is the role of motor cognition in perception?*

Motor cognition not only depends in part on representations created during perception, but also actually affects the case of engaging in some forms of perception. The brain has evolved specific neural mechanisms that detect and process the motion of other animals, including humans. In addition, human actions are processed differently than other types of biological motion. Crucially, the motor system is involved when we perceive actions that we can produce, which thereby makes it easier for us to use memories of previously observed actions to produce our own actions in the future.

Think Critically

- If a capacity is innate, does this mean that learning plays no role? If learning plays a role in detecting and processing biological motion, what role might it play?
- If you were temporarily paralyzed, do you think you could still perceive actions even if you couldn't produce them? If so, would this disprove the idea that the motor system is involved when we perceive actions?