

THEORETICAL AND REVIEW ARTICLES

Weaving the fabric of social interaction: Articulating developmental psychology and cognitive neuroscience in the domain of motor cognition

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In this article, we bring together recent findings from developmental science and cognitive neuroscience to argue that perception–action coupling constitutes the fundamental mechanism of motor cognition. A variety of empirical evidence suggests that observed and executed actions are coded in a common cognitive and neural framework, enabling individuals to construct shared representations of self and other actions. We review work to suggest that such shared representations support action anticipation, organization, and imitation. These processes, along with additional computational mechanisms for determining a sense of agency and behavioral regulation, form the fabric of social interaction. In addition, humans possess the capacity to move beyond these basic aspects of action analysis to interpret behavior at a deeper level, an ability that may be outside the scope of the mirror system. Understanding the nature of shared representations from the vantage point of developmental and cognitive science and neuroscience has the potential to inform a range of motor and social processes. This perspective also elucidates intriguing new directions and research questions and generates specific hypotheses regarding the impact of early disorders (e.g., developmental movement disorders) on subsequent action processing.

1. A Meeting of Minds: Integrating Developmental Science and Cognitive Neuroscience in the Domain of Motor Cognition

In the past decade, exciting new discoveries in developmental science and cognitive neuroscience have been made in domains such as action perception, theory of mind, and affective processing. Historically, research in these domains has proceeded along parallel paths, often addressing similar research topics and areas of inquiry. However, to date, communication between the two academic fields has been rare and limited (but see Decety & Jackson, 2004; Decety & Sommerville, 2003; and Saxe, Carey, & Kanwisher, 2004, for exceptions). Our intention in this article is to articulate new developmental data with cognitive neuroscience findings in the domain of motor cognition.

From our perspective, *motor cognition* refers to the way in which we think about and conceive of our own and oth-

ers' actions. We argue that much of how we think about others' actions, and in turn engage in social interaction, arises from the activation or simulation of our own motor representations (see Jeannerod, 2001). Thus, we consider motor cognition to encompass all the processes involved in the planning, preparation, and production of our own actions, as well as the processes involved in anticipating, predicting, and understanding the actions of others. We assume that processes operate primarily at the covert, automatic level and, as such, without our conscious awareness.

Our perspective in this article is consistent with recent theories of embodied cognition, an emerging theme in both cognitive science (Barsalou, 1999, 2003; Barsalou, Simmons, Barbey, & C. D. Wilson, 2003; Pecher, Zeelenberg, & Barsalou, 2004) and developmental science (e.g., E. Thelen, 1995; E. Thelen, Schöner, Scheier, & Smith, 2001). Traditional theories of cognition assume that knowledge consists of amodal redescription of sensory, motor, and introspective states (including emotions, affects, appetitive states, cognitive operations, and beliefs; see Barsalou, 1999) that originally accompanied an event or experience. According to these theories, knowledge exists independently of these states and operates accord-

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ing to different principles. In contrast, embodied theories of cognition construe knowledge as partial simulations of these sensory, motor, and introspective states (e.g., Barsalou, 2003; Barsalou, Niedenthal, Barbey, & Ruppert, 2003). One intuitive example is that empathy, or understanding another person's emotional state, comes from mentally "re-creating" this person's feelings in us (Decety & Jackson, 2004; Preston & de Waal, 2002). According to theories of embodied cognition, such an understanding emerges from simulation of bodily states in modality-specific brain areas (e.g., Barsalou, Niedenthal, et al., 2003). Thus, the claim made by modern embodiment theories is that all cognition, including high-level conceptual processes, relies heavily on such grounding in either the modalities or the body (M. Wilson, 2002).

In attempting to integrate developmental and neuroscience data, we do so with several caveats in mind. First, we interpret neuroscience findings on the basis of motor cognition with an appreciation that the brain basis of these processes may differ between adults and children. It is generally understood that there is a progression of maturation from posterior to anterior regions, with the primary visual cortex being functional from shortly after birth and the prefrontal cortex being the last part to become functional. Moreover, such a view is often assumed to have direct functional consequence (i.e., a unidirectional causal path from genes to structural brain changes to psychological function; Johnson, 1997). In contrast, another approach views interactions between genes, structural changes, and psychological functions as bidirectional (Gottlieb, 1992). This latter approach is considered to be a more appropriate way to view postnatal brain development (Johnson, 2000). However, almost all neuroscience findings discussed in this article originate from neuroimaging studies with adult participants. As such, caution must be taken in interpreting the brain bases of motor cognition in infants and children, and future research is necessary to establish continuity in the neural basis of motor cognition from developing to more mature forms of cognition.

Second, we acknowledge that determining the locus of neural activity during a given task does not necessarily provide information about the psychological processes involved in such a task. Nevertheless, it is our hope that the synthesis between developmental science and cognitive neuroscience will help to elucidate the nature of motor cognition and its role in other aspects of cognition and that such an integration will exert a reciprocal influence on developmental theorizing and in guiding investigations on the neural basis of motor cognition.

2. From Perception–Action Coupling to Action Representation: Evidence for Shared Representations

2.1. Action and perception are flip sides of a coin.

The continuity between different aspects of motor cognition is based primarily on perception–action cycles, which are the fundamental logic of the nervous system (Sperry, 1952). These processes are functionally intertwined:

Perception is a means to action, and action is a means to perception. Indeed, the vertebrate brain has evolved for governing motor activity with the basic function to transform sensory patterns into patterns of motor coordination. Gibson (1966) proposed the metaphor of "affordance" to account for the direct link between perception and action. Such affordances are the possibilities for use, intervention, and action offered by the local environment to a specific type of embodied agent. For example, a human perceives a garbage can as "affording the disposal of trash," but the affordances presented by a garbage can to a raccoon would be radically different.

Shepard (1984) argued that, as a result of biological evolution and individual learning, the organism is, at any given moment, tuned to resonate to the incoming patterns that correspond to the invariants that are significant for it. These patterns, according to Shepard, have become most deeply internalized (i.e., represented), and even in the complete absence of external information, the system can be excited entirely from within (e.g., while imagining). Thus, unlike Gibson (1966), Shepard makes explicit reference to internal representation and makes it possible to articulate the notion of resonance with that of motor representations. In addition, infants in postnatal life actively seek information about themselves and others, and they select appropriate inputs for the subsequent further specialization of the brain (Johnson & Morton, 1991). This latter aspect is compatible with contemporary theory of motor representations, which stresses the autonomy of the individual with respect to the external milieu and views his/her actions as a consequence of triggering by the environment or as a consequence of an internal process (Jeannerod, 1994). The concept of motor representations of action designate both (1) the mental content related to the goal or the consequences of a given action and (2) the operations that are supposed to occur before an action begins. There are no ontological reasons to consider these two levels of description as separate or, least of all, independent from one another.

2.2. Perception and action share a common computational code and underlying neural architecture.

In the past decade, growing numbers of results have been interpreted in favor of the common coding theory. This theory claims parity between perception and action. Its core assumption is that actions are coded in terms of the perceivable effects (i.e., the distal perceptual events) they should generate (Hommel, Müsseler, Aschersleben, & Prinz, 2001; Prinz, 1997). Performing a movement leaves behind a bidirectional association between the motor pattern it has generated and the sensory effects that it produces. Such an association can then be used to retrieve a movement by anticipating its effects (Hommel, 2004). These perception/action codes are also accessible during action observation (for a historical account of the ideomotor principle, see Stock & Stock, 2004). Observation of an action should activate action representations to the degree that the perceived action and the represented action are similar (Knoblich & Flach, 2003). Such a claim sug-

gests that we represent observed, executed, and imagined actions in a commensurate manner, and common coding theory makes specific predictions regarding the nature of action and perceptual representations. First, representations for observed and executed actions should rely on a shared neural substrate. Second, a common cognitive system predicts interference effects when action and perception attempt to access shared representations simultaneously. Third, such a system predicts facilitation of action based on directly prior perception, and a facilitation of perception based on directly prior action. As we discuss below, each of these predictions has been borne out in recent research findings.

2.2.1. Observed and executed actions rely on a shared neural substrate. A variety of electrophysiological research has demonstrated that two primary areas of the primate brain (ventral premotor cortex and superior temporal sulcus) are selectively activated during the observation of actions executed by conspecifics. Some of these cells (mirror neurons), in area F5 of the ventral premotor cortex, are sensorimotor neurons that fire both when the monkey executes certain kinds of actions and when the monkey perceives the same actions being performed by another (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Rizzolatti et al.'s (1996) findings provided the first convincing neurophysiological evidence for a direct matching between action perception and action execution. Umiltà et al. (2001) found that a subset of these mirror neurons also responds when the final part of an action, crucial in triggering the response when the action is seen entirely, is hidden and can only be inferred. Therefore, specific neurons in this region code the inferred goal of the action rather than the action itself. Automatically matching the agent's observed action onto the observer's own motor repertoire without the observer's executing it, the firing of mirror neurons in the observer's brain simulates the agent's observed action and thereby contributes to the understanding of the perceived action (Rizzolatti, Fogassi, & Gallese, 2004).

Kohler et al. (2002) extended this idea by showing that some neurons display mirror properties between motor and other modalities, such as audition. This demonstrates that single neurons are concerned with some actions regardless of the modality through which a given action is inferred (i.e., it is the consequence of the action that is represented). Such neurons are not restricted to the premotor cortex but have also been recorded in other areas of the brain—notably, in the posterior parietal cortex (area PF) in relation to actions performed with objects (Gallese, Ferrari, Kohler, & Fogassi, 2002). In a new single-cell electrophysiological study with monkeys, Fogassi et al. (2005) reported that inferior parietal mirror neurons, in addition to recognizing the goal of the observed motor acts, discriminate identical motor acts according to the action in which these acts are embedded. They further argued that because the discriminated motor act is part of a chain leading to the final goal of the action, this neuronal property allows the monkey to predict the goal of the

observed action and, thus, to “read” the intention of the acting individual.

Another cortical region that responds to the observation of others' actions is located in the superior temporal sulcus (STS). In the macaque monkey, Perrett et al. (1989) found that there are neurons in the superior part of the STS that are sensitive to the sight of static and dynamic information about the body. The majority of these cells are selective for one perspective view and are considered to provide viewer-centered descriptions that can be used in guiding behavior. For some cells in the lower bank of STS, the responses to body movements are related to the object or to the goal of the movements. Movements effective in eliciting neuron responses in this region include walking, turning the head, bending the torso, and moving the arms. A small set of STS neurons discharges during the observation of goal-directed hand movements (Perrett et al., 1989). Moreover, a population of cells, located in the anterior part of the STS, responds selectively to the sight of reaching but only when the agent performing the action is seen attending to the target position of the reaching (Jellema, Baker, Wicker, & Perrett, 2000). In addition, the responses of a subset of these cells are modulated by the direction of attention (indicated by the head-and-body posture of the agent performing the action). This combined analysis of direction of attention and body movements supports the detection of intentional actions.

It is noteworthy that, unlike neurons in areas F5 and PF, STS neurons do not appear to be endowed with motor properties. Rizzolatti, Fogassi, and Gallese (2001) suggested that the “action detecting” system in STS provides an initial “pictorial” description of the action that would then feed to the F5 motor vocabulary, where it would acquire a meaning for the individual and activate circuits comprising mirror neurons, which can, in principle, reproduce the perceived action. The two areas, STS and F5, are not directly connected, but both of them are linked to parietal lobule area PF, which projects to the premotor cortex.

In a neurometabolic study, Raos, Evangelidou, and Savaki (2004) used the quantitative ^{14}C -deoxyglucose method in monkeys who either grasped 3-D objects or observed the same movements executed by humans. They found that the forelimb regions of the primary motor cortex and the primary somatosensory cortex were significantly activated in both cases. The results of their study provide strong evidence for the use of primary motor cortex representations during the observation of actions and demonstrate that the observation of an action is represented in the primary motor and somatosensory cortices, as is its execution. The results also indicate that, in terms of neural correlates, recognizing a motor behavior is like executing the same behavior, requiring the involvement of a distributed system encompassing not only the premotor but also the primary motor cortex.

Common neural activation during action observation and execution has also been documented in humans. For instance, Hari et al. (1998) specifically examined the activity of the precentral motor cortex using magnetoencephalography (MEG) while subjects observed another

person manipulating an object and found that the activity was similar, but weaker in intensity, to that seen in motor cortex when subjects actually execute the action. Similarly, a handful of functional magnetic resonance imaging (fMRI) studies have demonstrated that a motor resonance mechanism in the premotor and the posterior parietal cortices also exists when subjects observe goal-directed actions executed by other people (e.g., Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Hamzei et al., 2003) or even when only the goal of these actions is visible (e.g., Chao & Martin, 2000; Grèzes & Decety, 2002). Such a system is present not only in adult brains but also in brains of young children. An electroencephalographic study with intracranial recordings on a 36-month-old child showed that corresponding areas of the sensorimotor cortex were activated when the child watched another person drawing with his right hand and when the child drew with her own right hand (Fecteau et al., 2004).

In addition, the activation pattern in the premotor cortex elicited by the observation of actions performed by another individual follows its somatotopic organization. Watching mouth, foot, and hand actions elicits different sites in the premotor and superior parietal cortices, which are normally involved in the actual execution of the observed actions (Buccino, Binkofski, & Riggio, 2001). In another domain, using transcranial magnetic stimulation (TMS), it has been found that listening to speech is associated with an increase of motor-evoked potentials recorded from the listeners' tongue muscles when the presented words strongly involve tongue movements when uttered (Fadiga, Craighero, Buccino, & Rizzolatti, 2002; Watkins, Strafella, & Paus, 2003).

Another compelling demonstration of the involvement of motor representations in the perception of bodily movements is provided by studies making use of the phenomenon of apparent motion. Stevens, Fonlupt, Shiffrar, and Decety (2000) adapted the apparent biological motion paradigm, originally developed by Shiffrar and Freyd (1990), to present subjects in the scanner with a human model in different postures. Depending on the activation conditions, subjects were shown either possible or impossible biomechanical paths of apparent motion. The left primary motor cortex and parietal lobule in both hemispheres were found to be selectively activated when subjects perceived possible paths of right-limb human movement. No activation in these areas was detected during conditions of impossible biomechanical movement paths.

Overlapping areas of neural activation are not limited to action observation and execution; they also extend to mental simulation of actions. Decety (1996) established that imagined and executed actions share a similar neural substrate: Neurodynamic increases were documented in the motor and parietal cortices that are similar to those seen during actual movement production. In addition, a number of studies have shown that the autonomic system responsible for heart and respiration adaptation to effort, not under voluntary control, presents visible changes during mental simulation of action involving graded changes in mental effort. For instance, when participants imagined

running at an increasing speed (Decety, Jeannerod, Germain, & Pastene, 1991) or pedaling at an increasing rate (Decety, Jeannerod, Durozard, & Baverel, 1993), highly consistent changes were found in heart and respiration rates, which correlated with mentally represented force. The absence of muscular activity during mental simulation was verified by measuring end-tidal PCO_2 and anaerobic muscle metabolism (using nuclear magnetic resonance spectroscopy).

Observation of actions performed by others seems also to involve central activation of the autonomic system. In one study, participants were requested to observe a scene in which an actor performs a running exercise at different speeds (Paccalin & Jeannerod, 2000). The respiration rate of the observers increased while they were watching the actor. Furthermore, the respiration rate of the observers correlated with the amount of effort produced by the actor (e.g., the respiration rate was higher during observation of the actor walking at 7 km/h than at 2.5 km/h). These findings demonstrate similarities in the central physiological mechanisms involved in mental simulation and action observation.

Furthermore, in a meta-analysis, Grèzes and Decety (2001) reviewed functional neuroimaging studies that examined the neural correlates of action observation, simulation execution, and verb generation of actions and found that action observation and execution, in particular, shared overlapping areas of neural activation in premotor and parietal cortices.

A recent study demonstrated that imagery of voluntary movement activates body-part-specific motor representations. Ehrsson, Geyer, and Naito (2003) asked subjects to imagine themselves performing finger and toe flexion and extension along with horizontal movements of the tongue. Activation maps were compared with functional images acquired when subjects were actually executing these movements. The authors documented that activation during motor imagery was specific to somatosensory and motor areas activated during actual motor execution. One TMS study provides converging evidence that action simulation recruits neural resources similar to those recruited by action execution and observation. Participants were asked to observe, imagine, or imitate hand actions while magnetic stimulation was delivered over the hand motor area of the left hemisphere and motor-evoked potential (MEP) recorded in muscles of the dominant hand (Clark, Tremblay, & Ste-Marie, 2004). Across all conditions, significant MEP facilitation was detected, a finding consistent with the proposal that perceived and imagined actions involve neural simulation.

Taken together, these findings provide evidence that neural representations used during action execution are also recruited during action observation and action simulation. As such, they raise the possibility that these representations play a functional role in how we conceive of others' actions. Recent behavioral research provides converging evidence that observed and executed actions are coded according to a common framework.

2.2.2. Action/perception inhibition. At a behavioral level, evidence suggests that interference occurs when ac-

tion and perception try to simultaneously activate the same code.

First, a number of studies have established impairments in perception during tasks in which subjects must act at the same time. When asked to identify arrow directions presented on a monitor using pre-prepared left- and right-key responses, subjects' ability to perceive the direction of an arrow is reduced when the response required matches the arrow direction (Müsseler & Hommel, 1997). The findings from these spatial compatibility tasks suggest that interference occurs because action and perception try to simultaneously access the same representation codes.

Hamilton, Wolpert, and Frith (2004) investigated participants' ability to judge the weight of a box lifted by an actor while participants were either lifting or passively holding a light or heavy box. The authors found that active lifting altered perceptual judgment. Participants were less accurate at estimating the weight of the actor's box during active lifting than during passive lifting. In addition, errors were biased in the direction opposite participants' box weight: Participants lifting a light box judged the actor's box to be heavier than it actually was. A recent study provides converging evidence for interference effects of self-action on observed action. Jacobs and Shiffrar (2005) report that observers' accuracy on a gait-speed discrimination task was poorer for walking observers than for bicycling or standing observers.

Similarly, interference effects of perceiving action on action production have also been documented. When subjects were required to execute a movement while simultaneously observing someone else executing an incongruent movement, interference effects were observed in the form of increased variance of movement (Kilner, Paulignan, & Blakemore, 2003). Interestingly, this interference occurred only when another human agent executed the incongruent movements and not when a robotic arm performed them. These findings suggest that simultaneous action execution and observation can produce interference effects and that the degree of such effects depends on the kinematics and visual similarity between the prime and the response.

A study conducted by Sebanz, Knoblich, and Prinz (2003) demonstrated that such interference effects persist in a spatial compatibility task distributed between 2 subjects such that each subject took care of one of two responses. In this task, subjects responded to two different colors using a buttonpress. In one condition, an individual produced a right-button press in response to one color and a left-button press in response to the other color. In another condition, this response was distributed across 2 individuals sitting next to each other such that each individual was only responsible for responding to one color. Color patches were accompanied by an irrelevant spatial cue that was either compatible or incompatible with the required response. Incompatible cues slowed response times for both the 1-person version of the task and the 2-person version of the task. These findings indicate that one's own actions and others' actions are represented and planned in a functionally equivalent way.

2.2.3. Action/perception facilitation. Prior motor observation also facilitates action production, suggesting that the perception of action primes a representation making it in turn more readily available to action. Viewing compatible motor responses prior to responding speeds action production, whereas viewing incompatible motor responses prior to responding slows action production (Brass, Bekkering, & Prinz, 2001), and observing prehension primes subsequent execution (Castiello, Lusher, Mari, Edwards, & Humphreys, 2002). Action production also affects action perception: Perceptual judgments of arm movements affect subsequent motor learning (Hecht, Vogt, & Prinz, 2001). Further work suggests that proprioceptive information concerning one's own body position influences visual perception of others' body positions (Reed & Farah, 1995).

This impact of action production on action perception is not unique to adults. In a recent study, Sommerville, Woodward, and Needham (2005) assessed 3.5-month-old prereaching infants' ability to perceive the reach of another person as object-directed using a visual habituation paradigm. Infants watched an actor reach for one of two toys on a puppet stage, repeatedly. After infants habituated to this event, the locations of the toys were switched, and infants saw events that were used to assess their ability to construe the actor's reach as goal-directed. On new object events, infants saw the actor reach to a new toy in the same location that she had reached to initially. On new side events, the actor reached to a new side of the stage for the same toy she had initially grasped. Infants provided with an intervention task that facilitated their ability to reach for and apprehend toys prior to the habituation paradigm looked longer at the new object events, indicating that they represented the reach as object-directed. In contrast, infants who received no action intervention prior to taking part in the habituation paradigm looked equally to both test events. These findings suggest that facilitating infants' goal-directed action production also impacts their perception of goal-directed actions performed by others, indicating that both action production and perception may be subserved by common representations.

Taken together, these findings suggest that observed and executed actions rely on a common neural and computational code. Research on neonatal imitation (e.g., Meltzoff & Moore, 1977) and emerging developmental work (e.g., Sommerville & Woodward, 2005a, 2005b; Sommerville et al., 2005) suggest that such a mechanism is present from very early in life and, through social interaction, may constitute a shared representational framework for one's own and others' actions (see Decety & Sommerville, 2003). In the following section, we explore the functional role of these shared representations in various aspects of motor cognition.

3. Shared Representations at Work: The Functional Consequences of a Common Coding System

The perception–action matching system offers a parsimonious explanation of how we represent the actions of

others, by a direct mapping of the visual representation of the observed action into our motor representation of the same action. Indeed, a number of recent reviews have raised the possibility of such an observation–execution matching system in action recognition and understanding (e.g., Blakemore & Decety, 2001; Buccino et al., 2001; Gallese, Keysers, & Rizzolatti, 2004; Rizzolatti & Craighero, 2004; M. Wilson & Knoblich, 2005), as well as in empathy (Decety & Jackson, 2004; Preston & de Waal, 2002). In this section, we marshal evidence to suggest that shared representations are involved in at least three aspects of motor cognition: action anticipation, action organization, and action imitation (see Figure 1).

3.1. Action anticipation. Our ability to navigate our environment relies in part on our capacity to anticipate what our social partners will do next. Action anticipation can serve a very basic and adaptive purpose: for instance, imagine your dinner partner eyeing your dessert plate hungrily then starting to move her fork in the vicinity of your brownie. Anticipating your partner’s next maneuver

can enable you to adjust your actions accordingly (in this case, to swiftly move your brownie out of reach). Some investigators have suggested that shared representations form the basis of our ability to predict the outcome of our own and others’ actions (e.g., M. Wilson & Knoblich, 2005).

There is evidence to suggest that individuals readily anticipate the next step of an action sequence. In one study, participants completed simple two-step action sequences in which they reached for and grasped a cube and then either transported it to a new location or merely lifted it up. The intended action influenced the time to apprehend the cube: Participants reached for the cube more quickly when they were required to transport a small cube to a new location than when they were required to merely lift a large cube (Johnson-Frey, McCarty, & Keen, 2004). Similar results have been documented in infants: The velocity with which infants reach for an object is influenced by whether they intend to subsequently throw or place the target toy (Claxton, Keen, & McCarty, 2003).

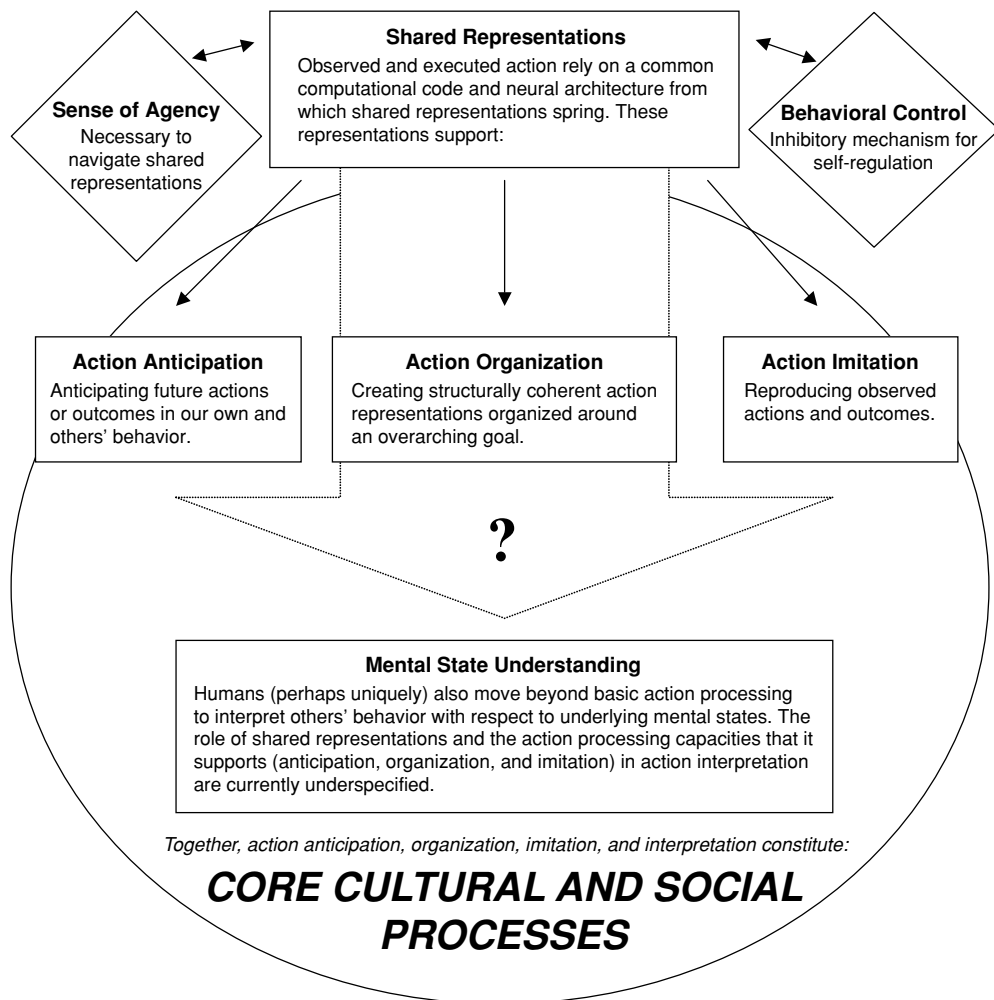


Figure 1. Components of motor cognition.

Action anticipation also extends to the actions of others. Infants expect an actor to move toward and contact an object that the actor previously looked at and positively emoted toward (Phillips, Wellman, & Spelke, 2002), and preschool children use an actor's eye gaze to predict the actor's goal (Baron-Cohen, 1995). Adults likewise predict the future actions of others on the basis of present actions. Participants can predict the second letter of a two-letter sequence when shown the emerging trace of the first letter at levels above chance (Orliaguet, Kandel, & Boe, 1997). Furthermore, participants' ability to detect whether a body posture demonstrates a possible or impossible configuration is primed by prior incomplete motion sequences (in which the motion sequence would have resulted in the test posture if the human model had continued the action), suggesting that individuals anticipate future body postures of an actor (Verfaillie & Daems, 2002).

In one initial positron emission tomography (PET) study, participants were scanned during the preparation and execution of hand movements (Krams, Rushworth, Deiber, Frackowiak, & Passingham, 1998). Preparation was associated with hemodynamic increases in the left inferior parietal cortex, the ventrolateral premotor cortex (including Broca's area), the primary motor cortex, the cerebellum, and the anterior cingulate cortex. All these regions, except the anterior cingulate cortex, pertain to the neural circuitry that mediates motor execution.

Further evidence suggests that individuals may use their own action plans when anticipating the actions of others. Using PET, Chaminade, Meary, Orliaguet, and Decety (2001) investigated regional cerebral blood flow during a task in which participants were asked to anticipate the outcome of a single moving dot trajectory depicting the beginning of mechanical, pointing, or writing movements. Left orbitofrontal and inferior frontal cortices were selectively activated when participants anticipated human action (e.g., the writing and pointing stimuli). Writing anticipation uniquely involved the left pars opercularis and the left superior parietal lobule, and pointing anticipation activated the left premotor area and right intraparietal sulcus (IPS). The frontoparietal circuits recruited by these tasks are also involved in the control of action in both monkeys and humans (Geyer, Matelli, Luppino, & Zilles, 2000), and the specific activation associated with writing anticipation (left premotor and right IPS) has been documented to be involved in the preparation and visual control of action, respectively (Desmurget & Grafton, 2003). These findings provide support for motor involvement in the anticipation of human action.

Another strong piece of evidence in favor of the involvement of the motor mirror system during the anticipation of someone else's action is provided by an electroencephalographic study in which participants were requested to watch video clips of a human model and a colored object (Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004). In half the video clips, after 1.5 sec, the hand moved and grasped the object; in the other half, the hand remained stationary. At the beginning of each clip, the color of the object indicated

whether the hand would subsequently move or not. Thus, the observed movements were entirely predictable from the color of object in the video. The participants' task was to detect differences in initial hand posture between the video clips (while the hand was stationary). The readiness potential, an electrophysiological marker of motor preparation, was present when participants were observing the actor's actions. More importantly, when the nature of and the onset time of the upcoming action were predictable, the rise of the readiness potential preceded the observed movement's onset. This suggests that knowledge of a coming action automatically activates the motor system.

Further evidence suggests that individuals process the actions of another person in a prospective manner much like their own actions. When observing a block-stacking task, the coordination between their gaze and the actor's hand is predictive, rather than reactive, and is highly similar to the gaze-hand coordination when the observers perform the task themselves (Flanagan & Johansson, 2003). These results indicate, in accordance with the common coding theory, that during action observation subjects implement eye motor programs directed by motor representations of manual actions. Consistent with this view, hemodynamic increases have been detected in the premotor cortex, the intraparietal cortex, the parietal operculum, and the inferior frontal gyrus when subjects observe grasping movements toward an object (e.g., Grèzes, Armony, Rowe, & Passingham, 2003). These regions were activated during actual execution of the same task but to a higher degree. Other studies have documented activation of the human motor system during both the preparation of self-actions and the anticipation of the actions of others (e.g., Ramnani & Miall, 2004). However, it should be noted that Ramnani and Miall found distinct action subsystems activated when subjects prepared their own actions and when they predicted actions of others.

3.2. Action organization. Our ability to perceive and represent the actions of others is not merely limited to anticipating the next upcoming action in a chain of events. Rather, we can also build representations of actions that are structurally coherent. Some have argued that these actions or event representations share many features and characteristics of object representations (e.g., Zacks & Tversky, 2001). Specifically, action representations reflect meaningful units and are hierarchically organized (i.e., they are organized with respect to an underlying plan or outcome).

3.2.1. Evidence for action segmentation across the lifespan. Action representations rely on our ability to segment action sequences into their constituent parts. Empirical work suggests that adults readily parse ongoing everyday behavior into meaningful units. For instance, when asked to segment a sequence of behavior, such as repairing a motorcycle, adult observers demonstrate strong agreement regarding the boundaries of units of action (e.g., Newton & Engquist, 1976). In order for us to understand the actions of others, we must segment action according to some conceptual framework.

Ongoing research suggests that adult action segmentations correspond to the completion of an actor's goal or intention. Baird and Baldwin (2001) showed adults digitized action sequences of continuous behavior (e.g., a woman cleaning her kitchen). The authors inserted tones in the presentation that either corresponded to the completion of a goal or intention (e.g., grasping a dish towel) or occurred at a midpoint in the behavior stream (e.g., reaching for the towel). The authors then investigated adults' memory for the tone locations, assuming that if adults parse ongoing behavior according to the actor's goals or intentions, then memory for tones indicating intention boundaries would be more accurate than would memory for tones that did not mark intention boundaries. Indeed, adults were significantly more accurate at remembering the location of tones that marked the completion of the actor's intention than at remembering the location of tones that did not. In addition, adults actually misremembered tones that occurred in midstream of behavior, stating that they occurred closer to the completion of the actor's intentions than in fact they did.

Similar segmentation abilities have been documented in infants. After watching the kitchen sequence described above, 10- and 11-month-old infants watched the same sequences with still frames inserted either after goal completion or in the midst of goal attainment (Baldwin, Baird, Saylor, & Clark, 2001). Infants reliably recovered attention to the goal-interrupting segments and not the goal-completing segments. Hence, even young infants possess the ability to parse ongoing action in ways that are commensurate with goal attainment.

3.2.2. Levels of action organization. Beyond parsing action into meaningful units, we organize actions within these units in a hierarchical manner. As adults, we can construe behavior at a variety of different levels, each of which may correspond to a different goal or intention. For instance, we can construe a single action (e.g., grasping a car door handle) at multiple levels of analysis: in terms of opening the car door, in terms of driving to the grocery store, or in terms of preparing for a family meal. Recent empirical evidence indicates that adults incorporate such structure in their action representations. For instance, Zacks, Tversky, and Iyer (2001) presented participants with videotapes of different everyday goal-directed activities (e.g., making a bed). Participants were instructed to segment all activities twice: once to produce the smallest units that were natural and meaningful, and once to produce the largest units that were natural and meaningful. Participants were able to segment action with respect to both levels, and their segmentations revealed a hierarchical relationship between unit types: Large-unit boundaries were disproportionately likely also to be small-unit boundaries.

The ability to organize action representations with respect to higher order goals is shared by children. Preschoolers spontaneously create hierarchically organized event schemas when asked about their everyday activities (e.g., Slackman, Hudson, & Fivush, 1986). When asked to imitate the actions of another person, preschoolers selec-

tively reproduce the highest order goal of the action (Bekker, Wohlschläger, & Gattis, 2000). In addition, preschoolers' and toddlers' memories for action sequences often exclude actions that do not bear directly on the goal of the sequence (Travis, 1997). Ongoing research suggests that 4-year-olds' ability to recall the agent of a given action within a sequence is heavily influenced by the temporal proximity of the action to the goal of the sequence: Agent recall decreases linearly with each step away from the goal (Sommerville & Hammond, 2005). These findings suggest that children construct action representations that are, in many ways, similar to those of adults.

Findings on the relative sophistication of children's action processing and representation have sparked interest in the roots of this ability. In a landmark study, Meltzoff (1995) showed 18-month-old infants a human actor attempting to produce a target action but failing. For instance, one of the sequences that toddlers viewed involved the actor trying to pull apart the ends of a miniature barbell. However, the actor's hands repeatedly slipped off of the barbell before he could complete the target action. Other infants watched the actor successfully complete the target action. When given the opportunity to act on the barbell, both groups of infants successfully reproduced the target action, despite the fact that the former group had never viewed this action. These findings suggest that 18-month-olds readily construed the actor's actions (grasping the barbell, pulling at the ends, etc.) with respect to an overarching goal.

3.2.3. Involvement of shared representations in action organization. Emerging evidence suggests that the ability to construct action representations centered around a higher order goal of a sequence may emerge at roughly 12 months of age, based at least in part on infants' own ability to produce similar action sequences. Using a visual habituation paradigm, Sommerville and Woodward (2005b) assessed 10- and 12-month-old infants' ability to represent a sequence in which an actor pulled a cloth supporting an out-of-reach toy as directed toward the ultimate goal of the sequence: the attainment of the toy. After watching an actor repeatedly pull a cloth and grasp the toy it supported, infants saw events in which the actor grasped a new cloth or directed her actions toward a new toy (e.g., grasped the same cloth as she had initially, which now supported a new toy). Twelve-month-old infants interpreted the actor's actions on only the cloth as directed toward the toy, indicating that they identified the higher order goal of the sequence. Interestingly, 10-month-old infants' ability to construct hierarchically organized representations of this sequence was related to their ability to solve a similar sequence in their own actions. These findings suggest that infants' own experience may play a formative role in the establishment of shared representations and that motor experience may be tightly linked to infants' ability to construct hierarchically organized action representations.

Work with adults also suggests that motor experience plays a formative role in establishing shared representations. For instance, an MEG study, conducted by

Järveläinen, Schürmann, and Hari (2004) monitored neural activity in the motor cortex while subjects watched an actor perform goal-directed and non-goal-directed actions with a pair of chopsticks. Observation of goal-directed tool use produced greater activation of motor cortex than did observation of nongoal-directed tool use, and the extent of activation was related to the amount of experience using chopsticks over the previous year. Furthermore, an fMRI study demonstrated that expert ballet dancers show stronger activation of premotor and parietal cortices when watching other ballet dancers than do novices. The extent of premotor and parietal activation in these areas was greatest when dancers observed their own style of dance relative to when they observed another kinematically similar dance style (capoeira; Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005).

In addition, recent evidence suggests that mirror system recruitment during action observation is mediated by the observers' species-specific motor history. Using fMRI, Buccino, Lui, et al. (2004) investigated neural activation to actions performed by humans and other species (a monkey and a dog). Frontoparietal circuits were selectively activated when the actions were part of the observers' motor repertoire (e.g., speech reading and biting) versus when they were not (e.g., barking).

These findings suggest that a species and individuals' motor history impacts the extent of mirror system involvement during action observation, raising the possibility that actions may be differently perceived, based on the individuals' motor capabilities and experience. Across a variety of domains, memory for action sequences is highly dependent on experience and expertise levels. For example, strong chess players are better at recalling chess game positions than are weak chess players (Gobet & Simon, 2000), and karate experts demonstrate better memory for karate techniques than do karate novices (Bedon & Howard, 1992). It is commonly believed that these memorial differences result from expert/novice differences in the segmentation of actions or events: Experts more readily organize their event representations into meaningful units than novices (see, e.g., Gobet et al., 2001). The greater mirror system involvement during action observation in experts than in novices may provide one mechanism by which experts' superior segmentation is supported.

Some have suggested that adult action parsing may rely on two different types of processes. Observers may use bottom-up processing to identify event boundaries (Zacks, 2004). For example, observers may utilize distinctive physical, motor, and sensory characteristics as direct cues to action boundaries. Alternately, or additionally, observers may recruit top-down knowledge structures, such as knowledge of an actor's intentions, to inform their action parsing (Baird & Baldwin, 2001; Zacks, 2004; Zalla, Pradat-Diehl, & Sirigu, 2003). Both of these types of cues have been demonstrated to correlate with event boundaries (see, e.g., Zacks, Braver, et al., 2001).

Few studies have examined the neural correlates of action segmentation. In one functional neuroimaging study, the sequential organization of events within a script was

considered as a means to explore the neurocognitive mechanisms involved in action organization (Ruby, Sirigu, & Decety, 2002). The scripts were composed of familiar goal-oriented sequences of events that typically occur in a systematic order. Study participants were required to judge whether or not the chronological order of these events was correct. In the left hemisphere, the supramarginal gyrus, the middle frontal gyrus, the inferior temporal gyrus, and the anterior cingulate cortex were activated when subjects organized the scripts into a coherent order. These results support the notion that frontal-parietal networks are engaged in short- and long-term script processing.

Using fMRI, Zacks, Braver, et al. (2001) revealed transient brain activity during segmentation tasks, indicating that people readily and spontaneously segment ongoing action. Two areas that have been implicated in human mirror system (superior temporal sulcus and premotor cortex) showed activation under passive viewing, and this activation increased significantly during active segmentation. Interestingly, the frontal region showed a reliable increase only when subjects segmented action at a coarse-grained level, whereas posterior regions (including superior temporal sulcus) increased reliably during active segmentation at both the coarse-grained level and the fine-grained level.

Zalla et al. (2003) have suggested that coarse-grained segmentation may primarily rely on conceptual knowledge, whereas fine-grained action segmentation may depend on sensitivity to sensory characteristics of action. These authors have speculated that parsing action into large units may recruit brain areas beyond the mirror system, including prefrontal areas involved in the planning and execution of actions. Zalla et al. compared action boundary detection in 9 patients with prefrontal lesions relative to that in 12 normal controls. Participants were asked to segment large and small action units. Prefrontal patients demonstrated impaired large event segmentation and preserved small event segmentation relative to controls.

These findings suggest that action organization may rely to an extent on shared representations for self and other actions. This may be particularly true when the action is one within the observers' own repertoire, when segmenting action into small units and for action sequences for which little or no preexisting conceptual knowledge exists.

3.3. Action imitation. A key part of social learning relies on our ability to reproduce the actions of our social partners. Existing evidence suggests that the ability to do so hinges on shared representations between self and other actions and that such an ability emerges early in life. Imitation appears to be present at birth: Neonates can imitate facial gestures presented to them (Kugiumutzakis, 1999; Meltzoff & Moore, 1977; Trevarthen, 1979). Over the course of the first year of life, infants imitate in an increasingly sophisticated and elaborate way. Infants progress from imitating facial expressions, to imitating actions on objects both immediately (Meltzoff, 1990), and after a delay (Collie & Hayne, 1999; Hayne, Boniface, & Barr, 2000), to reproducing the unseen goal of an action sequence (Meltzoff, 1995).

The direct perception–action coupling in the premotor/motor and posterior parietal cortices during action observation provides the basic mechanism for imitation. Interestingly, whereas many areas of the brain continue to undergo rapid growth during the first several years of life and reach their full maturation at adolescence, the premotor/motor and posterior parietal cortices appear to be fairly well developed at birth. Chiron et al. (1992) demonstrated that the primary somatosensory motor cortex shows higher relative regional cerebral blood flow (an index of brain maturation) at birth and requires a shorter time to reach normal adult values, suggesting a more advanced maturation of the motor regions. Giedd et al. (1999) assessed the volume of white matter and cortical gray matter in healthy children, and they found that the volume of white matter increased linearly with age, and the changes in volume of gray matter were nonlinear and regionally specific. Interestingly, the parietal cortex is mature before the frontal cortex.

Altogether, these neuroanatomical and functional data fit neatly with the early imitative abilities in neonates. The neural substrate that underpins the mirror system (which allows a direct matching between the action observation and its execution) seems in place early on. In addition, the prefrontal cortex, which underpins executive control and, notably, executive inhibition, is not fully mature immediately after birth. While cytoarchitecture reaches full development before birth in humans, the myelination of prefrontal connective fibers extends long after birth, until adolescence (Fuster, 1997). It can be suggested that this lack of inhibition on the mirror system at the beginning of childhood confers developmental benefits through neonatal imitation and motor mimicry. Then, inhibitory mechanisms progressively develop, in parallel to cognitive abilities (including more advanced forms of imitation such as deferred imitation) for which inhibition and working memory are requisite. However, this view of neonatal imitation as a simple mechanism based on motor resonance and a lack of inhibition implies that such behavior is automatic or reflex-like. Such a view contradicts the results of research showing that newborn children work themselves up toward a complete imitative response (Kugiumutzakis, 1993) or that some neonatal imitation can be seen as a form of delayed response (Meltzoff & Moore, 1994).

Two pieces of evidence suggest that our ability to imitate relies in large part on the existence of shared cognitive and neural representations of our own and others' actions. First, a number of studies have documented the involvement of the mirror system in action imitation. Second, imitation in humans appears to be selectively elicited by human stimuli. Each of these pieces of evidence is discussed in the preceding two sections.

3.3.1. Action imitation involves the mirror system. Some of the first neurophysiological evidence for the involvement of the mirror system during imitation of simple finger movements comes from an fMRI study by Iacoboni et al. (1999), in which individuals were tested in two conditions: observation only and observation execution. In the former condition, subjects were shown a moving finger, a

cross on a stationary finger, or a cross on an empty background. The instruction was to observe the stimuli. In the observation-execution condition, the same stimuli were presented, but this time the instruction was to lift the right finger, as fast as possible, in response to them. The results showed that the activity was stronger during imitation trials than during the other motor trials in four areas: the left pars opercularis of the inferior frontal gyrus (which is considered to be the homologue to F5 in the monkey), the right anterior parietal region, the right parietal operculum, and the right superior temporal region.

A series of neuroimaging studies revealed that the intention to imitate may exert a top-down effect on the brain regions involved in the observation of actions. Specifically, in addition to the areas typically activated during passive action observation, observation for imitation requires additional executive demands. In the scanner, participants were instructed to carefully watch pantomimed actions performed by a human model for either later recognition or imitation (Decety et al., 1997; Grèzes, Costes, & Decety, 1998). When observation of action conditions were contrasted with a baseline condition, in which static postures were shown, increased activity was detected in the premotor cortex at the level of the upper limb representation, the inferior frontal gyrus (Broca's area), the posterior STS, and the parietal cortex. When subjects observed actions for later imitation, as compared with passive observation of the same actions, a specific hemodynamic increase was detected in the supplementary motor area (SMA), the middle frontal gyrus, the premotor cortex, and the superior and inferior parietal cortices in both hemispheres. A different pattern of brain activation was found when subjects were observing actions for recognition. In that case, the parahippocampal gyrus in the temporal lobe was chiefly activated. Thus, the intention to imitate has a top-down effect on the information processing recruited in action observation. It requires additional processes of executive functions that are necessary to hold in working memory the actions perceived and also an inhibitory mechanism to refrain from imitating during the scanning period.

Using MEG, Nishitani and Hari (2000) investigated the cortical temporal dynamics of action representation during execution, online imitation, and observation of right-hand reaching movements that ended with a precision pinch of the tip of a manipulandum to determine whether these processes elicited similar neural activation in terms of both topography and timing. During execution, the left inferior frontal cortex was activated first (peak around 250 msec before the pinching); this activation was followed within 100–200 msec by activation in the left primary motor area and 150–250 msec later. During imitation and observation, the sequence was otherwise similar, but it started from the left occipital cortex. Activation was always strongest during action imitation. Only the occipital activation was detected when the subject observed the experimenter reaching his hand without pinching.

In a second study, Nishitani and Hari (2002) took neuromagnetic measures in participants who observed still pictures of lip forms, imitated them online, or made simi-

lar forms in a self-paced manner. In all conditions and in both hemispheres, cortical activation progressed in 20- to 70-msec steps from the occipital cortex to the superior temporal region (where the strongest activation took place), the inferior parietal lobule, and the inferior frontal lobe (Broca's area), and, finally, 50–140 msec later, the primary motor cortex. The signals of Broca's area and motor cortex were significantly stronger during imitation than were other conditions. These results demonstrate that still pictures, only implying motion, activate the human mirror neuron system in a well-defined temporal order.

In an fMRI study, Buccino, Vogt, et al. (2004) addressed the issue of imitation of a new skill. Musically naive individuals were scanned during four events: (1) observation of guitar chords played by a guitarist, (2) a pause following model observation, (3) execution of the observed chords, and (4) rest. The results showed that the basic circuit underlying imitation learning involves the inferior parietal lobule and the posterior of the inferior frontal gyrus plus the adjacent premotor cortex (mirror neuron circuit). This circuit starts to be active during the observation of the guitar chords. During the pause, the middle frontal gyrus (Brodmann area 46) plus the structures involved in motor preparation (dorsal premotor cortex, superior parietal lobule, rostral mesial areas) also become active. Buccino, Vogt, et al. proposed that, during learning of new motor patterns by imitation, the observed actions are decomposed into elementary motor acts that activate, via mirror mechanism, the corresponding motor representations in the parietal and ventral premotor cortices and in the inferior frontal gyrus. Once these motor representations are activated, they are recombined, according to the observed model, by the prefrontal cortex. This recombination occurs inside the mirror neuron circuit, with area 46 playing a fundamental orchestrating role.

Evidence for the involvement of the mirror system in imitation extends to imitation of facial expressions. Leslie, Johnson-Frey, and Grafton (2004) had subjects watch movies of facial expressions and hand movements while sitting passively and under imitative and motor control conditions. The authors documented activation of the left pars opercularis, the bilateral premotor areas, right STB, bilateral SMA posterior temporo-occipital, and cerebellar areas during both hand and face imitation. Interestingly, passive viewing of facial expressions selectively involved the right ventral premotor area, whereas imitation of facial expressions yielded bilateral activation.

Evidence suggests that individuals with autism may be impaired in their ability to imitate the actions of others. Williams, Whiten, and Singh (2004) reviewed 21 studies that investigated imitation in children with autism spectrum disorder. The authors concluded that children with autism do indeed exhibit an imitative deficit and that this deficit is best characterized as a difficulty in matching self-actions to the actions of others (as opposed to a motivational or executive function problem).

In a neuroimaging study, Nishitani, Avikainen, and Hari (2004) provided support for this proposal. They compared

healthy control subjects to subjects with Asperger's syndrome (who are impaired in social interaction and imitation) using MEG. Subjects were asked to imitate the lip gesture depicted in a still-face photograph. Abnormal imitation-related cortical activation sequences in the frontal and parietofrontal circuitry was observed, suggesting that shared motor representations dysfunction can account for a part of the imitative and social impairments in autism spectrum disorders.

In another fMRI study, Williams et al. (2006) have compared a group of autistic individuals with a control group in a finger movement imitation task. In comparing autistic subjects with healthy subjects, the authors found that autistic subjects had reduced hemodynamic activity in brain areas involved in movement analysis (visual cortex, temporoparietal cortex) and in areas underpinning the integration of this information into body knowledge (parietal cortex), action production, as well as mental state attribution (medial prefrontal cortex). Interestingly, this study did not replicate the activation in Broca's region in the control group, initially reported by Iacoboni et al. (1999). Williams et al. (2006) argue that the STS and inferior parietal cortex serves a self-other matching function between observed and executed actions by matching intentions across agents: It recognizes two different actions as similar even if they are achieved differently.

3.3.2. Imitation in humans is selectively elicited by human stimuli. A second piece of evidence that imitation relies on shared representations rests on the finding that imitation in humans is selectively elicited by human stimuli and that the neural signature of imitation appears to be selective to human models. For instance, young infants of 5 to 8 weeks old imitate tongue protrusion openings of a human model but not when an object performs this gesture (Legerstee, 1991), and older infants imitate the unseen target action of a human model but not an inanimate object (Meltzoff, 1995).

In adults, motor priming is specific to human forms. Castiello et al. (2002) explored the nature and specificity of motor priming by examining behavioral responses to actions produced by a robotic arm versus that produced by a human arm. The authors showed a priming advantage for the latter. Cerebral correlates of this effect seem to involve the premotor cortex and the right inferior parietal lobule, as demonstrated in an fMRI study conducted by Perani et al. (2001), who reported greater activity in these regions when subjects observed grasping movements executed by a human hand than when subjects observed the same actions performed by a virtual hand. Subsequent work by Castiello (2003) showed priming effects even when the kinematics of a model were not available, which suggests that the motor intention of conspecifics can be inferred from their gaze. In a follow-up fMRI study, Tai, Scherfler, Brooks, Sawamoto, and Castiello (2004) reported a selective activation of the left premotor cortex when participants observed a human model performing grasping actions. Interestingly, this activation was not evident for the observation of similar actions performed by a robot.

Not only is the tendency to imitate dependent on a human agent, but the similarity of the person to be imitated to the imitator also appears to affect the extent to which the actor's actions will be imitated and the accuracy with which they are reproduced. Ryalls, Gul, and Ryalls (2000) compared infants' imitation of peer versus adult actions. Fourteen- and 18-month-old infants were given the opportunity to reproduce a behavior that had previously been modeled by either a peer (a 3-year-old boy) or an adult. In both cases, the modeler had been trained on how to carry out the modeled sequences. When given the opportunity to reproduce the target action, infants exposed to the peer model performed more correct target actions than did infants exposed to the adult model. These findings fit nicely with the claim that activation of the motor system should be greatest when the observed actor and actions closely resemble those of the observer (e.g., Knoblich & Flach, 2001).

Certain characteristics of imitation appear to be unique to humans. These characteristics include the ability to separate means from ends and the ability to not only imitate but to recognize when others imitate us (Field, 1995; M. H. Thelen, Dollinger, & Roberts, 1975). These human specializations may rest on key differences in either the anatomy of the mirror system across species or additional brain areas that are recruited by these aspects of imitation.

3.3.3. Integral components of human imitation. The act of imitation itself includes (at least) two components: One component involves reenacting the goal of the action, and the other component involves reproducing the means by which the goal is achieved. Humans seem to have the unique ability to reproduce both the means and the goal even in the absence of the model and can do so flexibly given the context of the situation (Tomasello, 1999). For instance, in Nagell, Olguin, and Tomasello's (1993) study, 2-year-old children and chimpanzees watched a demonstrator use a rake-like tool to obtain a desirable out-of-reach object using one of two methods. Both groups benefited from the demonstration, but only children faithfully copied the demonstrator's methods of obtaining the toy. In contrast, although chimpanzees replicated the goal state, the methods that they used to do so were based primarily on the general functional relations of the problem and not the methods used to obtain the object. Subsequent work by Tomasello et al. (1997) revealed that the imitative abilities of nonhuman primates are restricted even when given the opportunity to imitate a conspecific (vs. a human) model.

The ability to distinguish means from ends in an imitative situation is present early in life. Carpenter, Call, and Tomasello (2005) engaged 12- and 18-month-old infants in an imitation game in which they watched a mouse hop across a mat either into a house or to a final location on the mat. Toddlers that saw the mouse hop into the house reproduced the final placement of the mouse but omitted the hopping action, whereas those that saw the final placement on the mat reproduced the behavioral means of the sequence. That is, both age groups flexibly interpreted the goal of the sequence dependent on the context.

Similar results have been documented in a study by Gergely, Bekkering, and Király (2002), in which 14-month-old infants saw an event in which a human actor activated a tap light using her head. If the reason that the actor failed to use her hands to activate the light was clear (e.g., she was holding a blanket around her body), toddlers imitated only the goal of the event. However, if it was not apparent why the actor used her head to activate the light, toddlers reenacted both the means and the goal (i.e., they used their heads to activate the light). These findings with typically developing children contrast with those of children with autism. Children with autism appear to be able to reproduce only the goal of an action sequence presented to them and not the means (Hobson & Lee, 1999). Taken together, these findings suggest that, although goals and means are closely intertwined in the act of imitation, they are, to some extent, dissociable and therefore may partly tap distinct neural processes. Furthermore, the same movement can realize several goals, and the same goal can be achieved through several movements; therefore, it is reasonable to assume that goals and movements are represented independently of each other (Prinz, 2003).

Support for this hypothesis comes from a neuroimaging study that examined the neural instantiation of processing the goal and the means (i.e., the movements) in an imitation paradigm (Chaminade, Meltzoff, & Decety, 2002). In this study, participants observed a human agent (only his hand and forearm were visible) building Lego block constructions, and they were asked to observe and imitate (1) the whole action performed by the experimenter (means and goal), (2) the goal only (end state of the object manipulation), or (3) the means only (the gesture without the last position). Partially overlapping clusters of activation were found in the right dorsolateral prefrontal cortex and in the cerebellum when participants imitated either the goal or the means, suggesting that these regions were involved in processing both aspects of the action. 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.

These findings support the idea that the means and the goal of imitation partially rely on dissociable circuits. Interestingly, the medial prefrontal activation during imitation of the means indicates that observing the means used by another individual prompts the observer to construct or infer the goal toward which the human agent is aiming. This region is known to play a critical role in inferring others' intentions and is consistently involved in mentalizing (i.e., the ability to understand that human actions are governed by mental states, such as beliefs, desires, and intentions; Frith & Frith, 2003). An alternative and complementary interpretation of the implication of the medial prefrontal cortex is based on the hypothesis that it contributes to goal achievement by three processes: goal-based action selection, rapid action evaluation, and discrimination of the early steps from the final steps toward the goal (Matsumoto, Suzuki, & Tanaka, 2004). This latter aspect is pres-

ent in conditions of imitation of the means without knowing the final position of the action made by the model.

Humans can also detect imitation and engage in reciprocal imitation. Agnetta and Rochat (2004) investigated infants' ability to distinguish between an actor that was imitating the infant and one that performed contingent but different actions on an identical toy. Infants (from 9 months of age) discriminated between the imitating and contingent experimenter. Toddlers can recognize that they are being imitated by another person and can begin to use mutual imitation as a communicative device (Asendorpf, Warkentin, & Baudonniere, 1988; Nadel, 2002). Interestingly, children with autism appear to be impaired in their ability to recognize that they are being imitated by another person (Nadel, 2002; Smith & Bryson, 1994). In adults, reciprocal imitation is associated with activation in the left STS and inferior parietal cortex, with the left inferior parietal cortex selectively activated when the participant is imitating another person and the right inferior parietal cortex selectively activated when the participant is imitated by another person (Decety, Chaminade, Grèzes, & Meltzoff, 2002).

Thus, findings from a range of imitation studies suggest that reproducing the actions of another person relies on the existence of a common neural and cognitive framework for observed and executed actions. Imitation cannot be reduced to the mere motor resonance between the self and the other (unlike motor mimicry); rather, imitation includes other components that usually fall under the umbrella of executive functions (e.g., selective attention, working memory, and inhibition). Byrne (2005) has argued that imitation can be decomposed into at least two different capacities: (1) social mirroring such that individuals match their actions to those of another (which has social benefits) and (2) learning by copying (which entails acquiring new behavioral routines through observation). It is likely that social mirroring is based on the mirror system, whereas learning by copying requires advance cognitive capabilities outside the scope of the mirror system. Furthermore, the aforementioned studies also suggest that the parietal cortex plays a pivotal role in imitation, possibly in distinguishing oneself from others, which is an essential aspect of the sense of agency (Decety & Sommerville, 2003; Jeannerod, 2003; Meltzoff & Decety, 2003; and see section 5.2 below).

4. Motor Cognition Provides the Fabric for Social Interaction

The findings discussed above provide evidence that the mirror system is involved in our ability to understand and anticipate the actions of others, represent those actions in a structurally coherent manner, and imitate the actions of others. Each of these abilities may in turn inform higher order social and cultural processes. Indeed, as pointed out by Chartrand and Bargh (1999), a large proportion of everyday human action may rely on these types of basic processes. Of course, this is not to say that all human social cognition relies on motor simulation (see Jacob & Jeannerod, 2004, for a critique of the motor theory of social cognition).

Below, we discuss the involvement of these processes in social facilitation and interpersonal coordination.

4.1. Interpersonal coordination. A key social process involves coordinating our actions with those of others. Consider moving a heavy item of furniture up a set of stairs with a friend. Integral to this interaction is our ability to not only react to immediate feedback given to us by our partner's actions (e.g., raising one end of the sofa in response to feeling our partner lift the other side) but also the ability to predict what our partner might do next (e.g., beginning to change the angle of the sofa as our partner approaches a turn in the staircase). Knoblich and Jordan (2003) investigated the ability of individuals to coordinate their actions with those of others in the context of an object tracking game. Individuals given external cues to their partner's action alternatives produced anticipatory strategies more readily than those who saw only the consequences of their partner's action selections and thus were more successful at object tracking task. These findings suggest that anticipation of others' actions facilitates group coordination, and one of the ways that such anticipation might be achieved is based on shared action representations.

4.2. Event understanding. Our tendency to build structured action representations may likewise serve a larger social purpose. The ability to organize actions with respect to an underlying plan might help one to build event schemas and to understand a variety of cultural conventions. Such a capacity may support the ability to produce and understand a variety of culture specific activities from simple tool use to sporting events and religious rituals. As previously suggested, the construction of shared representations may enable observers to parse or segment ongoing action into units that correspond to an actor's observable goals. This initial segmentation may pave the way for higher level conceptual processing, which could in turn modulate such segmentations facilitating event understanding. In keeping with this perspective, an fMRI study by Wood, Knutson, and Grafman (2005) revealed distributed neural activation in OFC, medial PFC, amygdala, anterior cingulate, and premotor cortex during a task in which participants were asked to evaluate simple events.

4.3. Social facilitation. Covert imitation (referred to as *mimicry*) may grease the wheels of social interaction. Chartrand and Bargh (1999) looked at nonconscious mimicry of the postures, mannerisms, and facial expressions of participants' social partners. When participants were instructed to work together on a task, their behavior tended to match that of strangers, unbeknownst to the participants. Chartrand and Bargh, in a second experiment, established that this nonconscious mimicry may actually play a functional role: Participants rated confederates that copied their posture and body movements as more likeable than those that did not. Finally, these researchers established that unconscious mimicry was more common in individuals who were highly empathic.

In line with these social psychology results, a number of studies have demonstrated that watching facial expression of emotions prompts the observer to resonate with

the state of another individual, with the observer activating the motor representations and associated autonomic and somatic responses that stem from the observed target (i.e., a sort of inverse mapping; Decety & Jackson, 2004). For example, while watching someone smile, the observer activates the same facial muscles involved in producing a smile at a subthreshold level, and this creates the corresponding feeling of happiness in the observer. In an fMRI experiment, Carr, Iacoboni, Dubeau, Mazziotta, and Lenzi (2003) showed that when participants are required to observe or to imitate facial expressions of various emotions, increased neurodynamic activity is detected in the superior temporal sulcus, the anterior insula, and the amygdala, as well as in areas of the premotor cortex corresponding to the facial representation.

4.4. Online social interpretation. Two recent studies documented activation of the motor system during tasks in which subjects were required to anticipate (Ramnani & Miall, 2004) or observe the actions of another person and make an inference about his or her mental state (Grèzes, Frith, & Passingham, 2004). However, the two studies differed in their results. Ramnani and Miall found that areas within the action control system are activated when predicting others' actions, including areas involved in theory of mind (i.e., paracingulate cortex and posterior STS), but a different action subsystem is activated when preparing one's own actions (dorsal premotor cortex). Only in this latter case was there a similarity between the neural circuits involved in one's own production and simulation. Grèzes et al. (2004) reported that the neurodynamic activity starts earlier in a number of cortical regions involved in motor control (namely, the dorsal premotor cortex, left parietal cortex, and right cerebellum) when participants made judgments about their own actions and those of others. In addition, this study reported that the onset of the hemodynamic response within the shared cortical network starts earlier for the self than for others. This latter finding may be an important aspect to distinguish one's own actions from the actions of others.

To investigate the neural mechanisms mediating the understanding of the intentions of others while watching their actions, Iacoboni et al. (2005) asked participants to watch three kinds of stimuli: grasping hand actions without a context, context only (scenes containing objects), and grasping hand actions performed in two different contexts. In the latter condition, the context suggested the intention associated with the grasping action (either drinking or cleaning). Actions embedded in contexts, compared with the other two conditions, yielded a significant signal increase in the posterior part of the inferior frontal gyrus and the adjacent sector of the ventral premotor cortex where hand actions are represented. Thus, premotor mirror neuron areas—areas active during the execution and the observation of an action—previously thought to be involved only in action recognition are actually also involved in understanding the intentions of others. Iacoboni et al. proposed that to ascribe an intention is to infer a

forthcoming new goal, and this is an operation that the motor system does automatically.

4.5. Social and cultural learning. Imitation is also an important social learning tool. This is true with respect to both our ability to learn specific problem solving strategies and our ability to internalize larger cultural activities and values. For example, 2-year-old children can reproduce a complex sequence of actions in order to open a box, particularly if they are given information about the goal of the action sequence beforehand (Carpenter, Call, & Tomasello, 2002).

Functional equivalence between one's own actions and others' actions may also provide a means for learning socially or culturally specific activities. In Somerville and Hammond's (2005) study, 4-year-old children constructed a set of toys using instructions either in collaboration with an adult experimenter (high-collaborative condition) or alongside an adult experimenter (low-collaborative condition). Under high-collaborative conditions, children often confused who had performed which actions during the toy-building sequences and showed a bias to overclaim the actions of the experimenter as performed by themselves. Children in the low-collaborative condition were more accurate at recalling who had done what during the toy-building sequences and showed no bias in their memory reports. When asked to reconstruct the toys all on their own, children in the high-collaborative condition outperformed children in the low-collaborative condition. These findings raise the possibility that certain task characteristics may cause children to anticipate the actions of others and misrecall who performed a given step of the sequence. Interestingly, this anticipation process may actually facilitate overall recall of the sequence.

Finally, action imitation may serve not only as a means to internalize the actions of others but also as an internalization process for larger cultural values. Forman, Aksan, and Kochanska (2004) found that 14- and 22-month-old infants imitated their mothers' behaviors (matching both behavior and motivation), thus predicting conscience at 33 and 45 months of age, as measured by internalized conduct and guilt.

5. Beyond Shared Representations: Behavioral Regulation, Establishing Agency, and Mental State Understanding

Given commensurability between one's own actions and others' actions, key additional processes are necessary for successful social interactions. The first concerns how individuals refrain from reproducing others' behavior if action representations are automatically activated. The second concerns the ability to establish agency in the face of shared representations. The third concerns how we move beyond analysis of the perceptually available aspects of actions to interpret behavior with respect to mental states. Although each of these processes lies outside the scope of the mirror system itself, each must interact with the mirror system at some level.

5.1. The role of inhibitory mechanisms in self-regulation. If one accepts that perception of others' actions triggers one's own motor representation, there must be some mechanisms to inhibit the action in the observer. One possible explanation is that, most of the time, the mere observation activates motor representations at a subthreshold level, enough to lead to motor priming, as demonstrated by behavioral studies (e.g., Brass, Bekkering, Wohlschläger, & Prinz, 2000), but not sufficiently to elicit the overt behavior. Another explanation is that a component of executive control (cognitive inhibition) is at play.

Substantial evidence for the inhibitory role of the prefrontal cortex has been reported in patients with large, bifrontal damage from degenerative and diverse mass lesions, who exhibit unsuppressed imitation or utilization behavior. For example, Lhermitte, Pillon, and Serdaru (1986) proposed that prefrontal cortex damage resulted in the loss of inhibitory control, a deficit in response inhibition. Consequently, the parietal lobe was released to engage whatever came within its perceptual sights, leading to a behavioral pattern of environmental dependency. However, neither the parietal association nor prefrontal cortices have direct projections to primary motor cortex or spinal cord. Access is dependent on premotor structures, including the rostral region of the SMA in the medial aspects of the superior frontal gyrus. Neuroimaging studies have pointed to a trend for medial premotor cortex dominance in internally guided action and the lateral premotor cortex in externally guided action (Schubotz & von Cramon, 2003). In terms of proposed lesion effects, medial premotor damage causes impairment of endogenously driven motor control, effecting a "release" of exogenously driven premotor system responses to perceived objects. The loss of internally driven and inhibitory control may underlie what patients describe as the feeling of being compelled to use objects (i.e., utilization behavior). This refinement of frontal–parietal mechanisms opens up new ways not only for interrelating diverse motor release deficits and motor control mechanisms but also for considering the subcortical–cortical and cortico–cortical neural networks subserving self-regulation and how humans balance internally driven and externally activated motor behaviors in order to achieve goals within complex and changing environments (Decety, in press).

Brass et al. (2001) carried out an fMRI study in order to investigate the cortical mechanisms underlying the inhibition of imitative responses. They employed a simple response task in which subjects were instructed to execute predefined finger movements (tapping or lifting of the index finger) in response to an observed congruent or incongruent finger movement (tapping or lifting). The comparison of brain activation in incongruent and congruent trials revealed strong activation in the dorsolateral prefrontal cortex (middle frontal gyrus) and activation in the right frontopolar cortex and the right anterior parietal cortex, as well as in the precuneus. These results support the assumption of prefrontal involvement in response inhibition and extend this assumption to a "new" class of prepotent responses—namely, to imitative actions.

5.2. The sense of agency. Given shared representations for one's own and others' actions, an additional mechanism outside the mirror system is necessary to differentiate self from others. The ability to recognize oneself as the agent of a behavior is the way one builds as an entity independent from the external world (Jeannerod, 2003). Agency plays a pivotal role in the development of cognition and a first level of self-awareness (or pretheoretical experience of one's own mentality) on which a theory of mind must be grounded. It has been proposed that from birth, and long before mirror self-recognition, infants develop a sense of self as a differentiated and situated entity in the environment via the active process of intermodal perception and exploration (Neisser, 1991). For instance, Rochat and Hespos (1997) demonstrated that neonates discriminate between external and self-stimulation. Rochat and Hespos observed newborn infants when they spontaneously brought one hand to the face, touching one cheek (self-stimulation) and when the experimenter's index finger touched one of the infants' cheeks (external stimulation). Microanalysis revealed that infants responded differently to the two types of stimulation. Newborns tended to display significantly more rooting responses (i.e., head turn toward the stimulation with mouth open and tonguing) following external stimulation than following self-stimulation.

A number of functional imaging studies have pointed out the involvement of the right inferior parietal lobule in this process (attribution of an action to its proper agent). The integration of visual and somatosensory signals processed in the parietal–occipital junction around the angular gyrus confers on this region a role in the elaboration of an image of the body in space and in time. Attribution of action to another agent has been associated with specific increased activity in the right inferior parietal lobe. For instance, Farrer and Frith (2002) instructed participants to use a joystick to drive a circle along a T-shaped path. They were told that the circle would be driven either by themselves or by the experimenter. In the former case, participants were requested to drive the circle, to be aware that they drove the circle, and, thus, to mentally attribute the action seen on the screen to themselves. In the latter case, they were requested to perform the task, but they were aware that the experimenter drove action seen on the screen. The results showed that being aware of causing an action was associated with activation in the anterior insula, whereas being aware of not causing the action and attributing it to another person was associated with activation in the right inferior parietal cortex.

Farrer et al. (2003) used a device that allowed modifying the participants' degree of control of the movements of a virtual hand presented on a screen. Experimental conditions varied the degree of distortion of the visual feedback provided to the participants about their own movements. The results demonstrated a graded hemodynamic activity of the right inferior parietal lobule that parallels the degree of mismatch between the executed movements and the visual reafference. In addition, studies on imitation have documented involvement of right inferior parietal cortex during reciprocal imitation, in which it may be

difficult to keep track of agency (Chaminade & Decety, 2002; Decety et al., 2002). The mechanism that accounts for the correct attribution of actions and thoughts to their respective agents appears to also be involved when one mentally simulates actions for oneself or for another individual. Ruby and Decety (2001) instructed participants to imagine actions either from the first-person perspective or from the third-person perspective. The first-person perspective was associated with specific increase in the left parietal lobule. By contrast, the third-person perspective resulted in activation in the right inferior parietal lobule. Similar specific increase in the right inferior parietal lobule at the border with the posterior STS was reported in studies investigating empathy, when participants imagined the feelings or the pain of others versus their own feelings of pain (e.g., Jackson, Brunet, Meltzoff, & Decety, 2006; Ruby & Decety, 2004).

It was suggested that agency judgments about who has performed an act are likely to be made on the basis of central representations coded in allocentric coordinates (Jeannerod, 1999). A common coding system of this kind is needed, since it is not possible to represent the actions of others in the egocentric coordinates used for generating our own actions (Farrer & Frith, 2002). There is strong physiological evidence that the inferior parietal cortex implements the kind of remapping process (Andersen, Essick, & Siegel, 1985) that would be needed to generate representations of body movements in allocentric coordinates.

Further evidence for the role of the right inferior parietal cortex in the sense of agency has been provided by neuropsychological studies in humans (e.g., Kinsbourne, 2002). Blanke, Landis, Spinelli, and Seeck (2004) studied out-of-body experiences (i.e., the experience of dissociation of self from the body) and autoscopia (i.e., the experience of seeing one's body in extrapersonal space) in 5 neurological patients and found that, for all of these patients, damage or dysfunction could be localized to the temporoparietal junction. In addition, Blanke, Ortigue, Landis, and Seeck (2002) found that direct cortical stimulation of this region in neurological patients induced out-of-body experience. While the left parietal region is involved in somatic experience in relation to action, the right region seems to also be involved in somatic experience but related to awareness. It is also associated with body knowledge and self-awareness, and its lesion can produce a variety of body representation-related disorders, such as anosognosia, asomatognosia, and somatoparaphrenia (Berlucchi & Aglioti, 1997). Finally, individuals who experience abnormalities in attribution of intention, such as schizophrenic patients experiencing passivity phenomena, exhibit dramatic activation of the right inferior parietal cortex when they generate actions (Spence et al., 1997). Interestingly, measurements of cerebral metabolism in children (between 18 days and 12 years of age) indicate a right hemispheric predominance, mainly due to the neural activity in the posterior associative areas of the parietal cortex (Chiron et al., 1997). Taken together,

these findings indicate a neural mechanism by which self-actions and others' actions are distinguished and that this neural mechanism appears to be present early in life.

5.3. Mental state understanding. As humans, our action analysis moves beyond anticipating others' actions, building structured action representations, and incorporating those actions into our own behavioral routines. We also have a tendency to interpret the actions of others, and we tend to do so with respect to underlying mental states. That is, we have a *deeply intentional* understanding of the behavior of others (cf. Chartrand & Bargh, 1999). Children start to use mental states to describe others' behavior at about 3 years of age (Bartsch & Wellman, 1995), and roughly a year later they understand that behavior can be motivated by beliefs that may or may not reflect the current state of reality (Gopnik & Astington, 1988; Wellman, Cross, & Watson, 2001; Wimmer & Perner, 1983). Adults also use a range of mental state constructs to describe and explain behavior, and this is true across cultures (D'Andrade, 1987). Indeed, the tendency to describe behavior with respect to various mental states is so entrenched that adults and children even use mental state language to describe the movement of animated objects (Berry & Springer, 1993; Heider & Simmel, 1944). Some scholars have suggested that this ability is a human cognitive specialization (e.g., Povinelli, 2000). One important question is whether the perception-action matching mechanism and its product—shared motor representations—can account (or to what extent it does) for the attribution of mental states to others.

Several authors have suggested that the shared representations network that stems from the perception-action matching mechanism may support mental state attribution via simulation (e.g., Blakemore & Decety, 2001). Such a proposal is in keeping with theories in philosophy of mind that postulate that action understanding is based on offline reproduction of behavior and introspection (e.g., Goldman, 2002; Gordon, 1986; Harris, 1989; Heal, 1998). Some authors have suggested that the mirror system may serve as an evolutionary building block or precursor to mental state understanding that facilitates social communication (e.g., Gallese & Goldman, 1998) or that basic action analysis abilities (e.g., behavior parsing) may be a necessary preliminary to the later development to attribute intentions and causes to observed actions (Byrne, 2003). In contrast, other authors have suggested that the mirror system's primary function concerns more basic aspects of action analysis (Keyesers & Perrett, 2004; M. Wilson & Knoblich, 2005). Finally, it has been proposed that the mirror system is part of a much wider system, which has at least three levels: (1) automatic contagion from movements as long as these are made by biological entities, (2) mirroring of specific goal-directed actions, and (3) a higher level at which intentions are mirrored (Blakemore & Frith, 2005).

Saxe (2005) has argued that the mirror system and the mentalizing system are two distinct processes, and it is likely that the former cannot account for mental state un-

derstanding. Numerous functional neuroimaging studies of mental state attribution across a variety of tasks (false belief understanding, attribution of intentions, mentalistic descriptions of object motion, evaluation of others' knowledge states, etc.) have documented several cortical areas outside of the classic mirror system that are reliably activated during mental state reasoning tasks: the right posterior STS, temporal poles, the amygdala, and the medial prefrontal cortex (see Frith & Frith, 2003, and Siegal & Varley, 2002, for reviews). Moreover, studies with patients have shown that damage to several regions in the prefrontal cortex impairs theory-of-mind abilities (e.g., Happé, Brownell, & Winner, 1999). Such findings suggest that support for the claim that the mirror system alone cannot support mental state attribution. Thus, two important questions in this area remain unresolved. The first concerns the potential developmental relation between the mirror system and the mentalizing system. The second concerns the computational role that each of the aforementioned areas plays in mental state attribution and whether any one of these areas is uniquely dedicated to mental state reasoning per se.

6. Future Directions

The research reviewed above suggests that shared representations for observed and executed actions may subservise a range of motor cognition processes. These processes in turn provide the fabric of social interaction. Below, we consider potential future directions for collaborations between developmental psychologists and cognitive neuroscientists.

First, we have suggested that the mirror system in humans supports action anticipation, structural organization, and imitation. Future research can address whether additional processes that are integral to motor cognition are also supported by such a system and the species specificity of such processes. In addition, interesting questions arise with respect to the range of motor acts and activities that elicit mirror activation in humans and nonhuman primates.

Second, the preceding section suggests that the areas outside the mirror system are integral to behavioral regulation, establishing agency and mental state understanding. As mentioned previously, the computational role that each neural area implicated in mentalizing remains to be determined. In addition, the contribution of the mirror system and its role in such high-level interpretation are currently underspecified.

Investigating more basic aspects of action analysis and higher level interpretation of human behavior in populations with developmental disorders may shed light on some of these questions. Indeed, this work has already begun. Diamond (2000) has suggested that motor development and cognitive development are more interrelated than was previously thought. For instance, motor coordination problems are common in children with ADHD. These children tend to have motor problems associated with cerebellar dysfunction. Several investigations have reported that the cerebellum is smaller in ADHD children than in healthy controls (e.g., Mostofsky, Reiss, Lockhart,

& Denckla, 1998), as well as a significant size reduction in frontal cortex (e.g., Filipek et al., 1997).

Children with autism demonstrate core deficits in the domain of social cognition. Research in this area is currently focused on whether children with autism exhibit deficits in mental state reasoning alone (Baron-Cohen, 1995) and in action analysis more broadly (Avikainen, Kulomaki, & Hari, 1999; Williams, Whiten, Suddendorf, & Perrett, 2001) or whether the observed social deficits associated with autism may result from more general attentional dysfunction (Allen & Courchesne, 2003; Happé, Briskman, & Frith, 2001). These issues can be difficult to pursue in children with autism because of the high coincidence of autism and mental retardation and because of the language difficulties often seen in children with autism.

Researchers are also pursuing neural and anatomical differences between children with autism and typically developing children. There is evidence of a reduced cerebellum in autistic individuals (e.g., Courchesne, Yeung-Courchesne, Press, Hesseline, & Jernigan, 1988), as well as a delayed maturation of the frontal cortex (Zilbovicius et al., 1995) in autistic individuals. In a functional imaging study, Zilbovicius et al. (2000) found that autistic children have a significant hypoperfusion in the temporal cortex, centered in a multimodal association region that is strongly connected with frontoparietal and limbic regions. This metabolic dysfunction was more pronounced in the right hemisphere.

We suggest that another population in which such questions can be investigated include adults with acquired neurological disorders and children with movement disorders. Parkinson's patients demonstrate disruptions of motor imagery at both a behavioral and a neural level (Dominey, Decety, Broussolle, Chazot, & Jeannerod, 1995; Thobois et al., 2000). In addition, a recent review concluded that individuals with Parkinson's disease also show deficits in theory of mind performance (Yoshimura & Kawamura, 2005). Emerging evidence suggests that children with developmental coordination disorder show impairments in motor imagery (P. H. Wilson et al., 2004), and motor imagery training can be effective in motor skill acquisition in children with impaired motor coordination (P. H. Wilson, Thomas, & Maruff, 2002). Moreover, children with cerebral palsy are delayed in succeeding at theory-of-mind tasks (Falkman, Sandberg, & Hjelmsquist, 2004). Individuals with movement disorders may demonstrate impairments in various aspects of social cognition either due to the role of contribution of motor cognition in social cognition or due to the fact that the nature of their disorder may change the manner in which others interact with them. Thus, research with this population will further theorizing about the role of the mirror system in action understanding and will help to further delineate the contribution of social experience to developing an understanding of others' actions and behavior.

7. Conclusions

Motor cognition arises from an automatic linkage between perception and action and represents a powerful en-

gine for social cognition. The mirror system provides the basic mechanism by which we implicitly and seamlessly relate with others (see Figure 1) and plays an essential role in social interaction, providing the basic building blocks for action analysis and in turn influencing a host of social processes. Early imitation shows that the understanding of other people is primarily a form of embodied practice and that we are selectively attuned to other conspecifics. Given such automatic activation of the self, it can be used as an analog for others in making predictions about them because of the similarities between ourselves and others. However, our ability to successfully navigate our social environment relies on additional processes. Specifically, commensurability between our own and others' actions requires that we have mechanisms for successfully distinguishing ourselves from others and for inhibiting our own actions when they are not adaptive. In addition, a key aspect of social cognition in humans involves the ability to reason about the mental states of others, an ability that relies on a range of capacities, including the capacity to use a general set of concepts applicable to individual minds, not simply an experience of one's own mind (Wellman, 1990). How these mechanisms and capacities mediate, constrain, and interact with the mirror system is currently underspecified and an important topic for future inquiry.

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