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## CHAPTER 11

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# A Cognitive Neuroscience View of Imitation

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In recent years, there has been a great upsurge in the neurophysiological investigations of imitation, particularly because new neuroimaging methods have become available to look at the anatomical areas involved in the perception-action coupling under diverse sophisticated paradigms. In addition, the discovery of mirror neurons in the monkey has provided a physiological model for the basic mechanism of perception-action coupling that is involved in imitation and action understanding.

The chapter begins by defining imitation. Then it reviews the neural mechanism for perception-action coupling and its link with motor representations both in monkeys and in humans. This coupling mechanism explains motor priming and social facilitation. Next, neuroimaging studies of imitation are discussed with a special section on imitation and emotion processing. It is then argued that executive inhibition is an important component of imitation. Neuroimaging research concerning reciprocal imitation and the sense of agency are presented. Finally, I discuss some important questions for future direction, notably whether brain systems involved in representing goal-directed action are distinct from the brain regions associated with mentalizing.

One critical aspect of functional imaging research is that data do not make much sense if they are not framed within a cognitive model of imitation leading to specific predictions about its neural implementation. Thus, a first requirement is to use a clear definition of what imitation is and what functions it subserves. Indeed, there are a variety of behaviors that have been indistinctively categorized under imitation. Yet, do flocks of birds acting together, people in conversation that synchronize their speech rate and body mannerisms, ballet dancers performing in unison, or an individual learning fencing account for the same phenomena? Are these different behaviors mediated by the same mechanism?

All theorists of human imitation acknowledge that it is an incredibly powerful way to learn skills and develop a sense of self, an important form of communication, a milestone in the development of intentional communication and more generally social interaction (e.g., Meltzoff & Gopnik, 1993; Nadel, Guérini, Pezé, & Rivet, 1999; Rogers, 1999). Despite the fact that there are many definitions and disagreements over what is imitation, most scholars agree that it is a natural mechanism that involves perception and action coupling for mapping one's own behavior onto the behavior observed in others, and that it serves an adaptive function. Indeed, imitation is a powerful mechanism for individual learning, which gives a level of flexibility that does not require the genetic predisposition to match the nature of the environment in which the individual will have to survive (Zentall, 2003). However, such a minimal definition of imitation is not sufficient to fully account for its role in human social development, if one appreciates that imitation allows individuals to ascribe internal experience to both themselves and others (Mitchell, 1993), is a mechanism for developing theory of mind (Meltzoff & Gopnik, 1993), a precursor for empathy (Trevvarthen, 1979), or a critical means to develop awareness of self-other coordination (Rogers, 1999). In addition, in humans, imitation is likely to depend on the motivation of the observer to attend to the behavior of the model.

In this chapter, rather than considering imitation as a simple matching mechanism, it is viewed as a molar construct, which includes different subcomponents such as perception-action coupling, visual attention, short-term memory, body schema, mental state attribution, and agency. These components rely on distributed network connectivity as demonstrated by a number of brain imaging studies that are discussed here. Each component of the network computes a different aspect of imitative behavior, and together the network orchestrates the task. The role of neuroscience is to help to identify the mechanisms responsible for imitation and decipher the contribution of each of its components. However, the various forms of imitation—ranging from copying a movement after seeing it done to reproducing an action intentionally offline—may well constitute a continuum from simple acts to complex ones, from unconscious mimicry to intentional reproduction, as well as from familiar actions to novel actions. This view of imitation is compatible with the idea of a hierarchy of mechanisms. Table 11.1 summarizes a number of apparently competitive theories of imitation and how these theories can be associated to specific brain mechanisms.

A first glance shows that there are more similarities than differences between these theories. In fact major disagreements seem to arise from the level (or definition) of imitation that is being used (e.g., simple vs. complex actions, immediate vs. deferred imitation). But again, one may view these various behaviors on a continuum that ranges from response facilitation (i.e., the automatic tendency to reproduce an observed movement) to learning a new behavior that is not present in the motor repertoire. It will be argued that the basic neural mechanism that unifies this variety of phenomena relies on the

**TABLE 11.1. Different Theoretical Accounts of Imitation, and Their Putative Neural Underpinnings**

- Byrne and Russon (1998) distinguish two processes involved in imitation: (1) the action level that allows one to copy actions following the surface form, and (2) the program level that allows one to copy the hierarchical organization of a complex action and ultimately learn new behavior. The system of mirror neurons may provide the neural basis for the former process.
- The direct mapping approach states that the motor system is activated by the perception of an action performed by another individual (Butterworth, 1993). Evidence from mirror neurons in the premotor cortex and parietal cortex seems sufficient to account for that theory.
- The active intermodal matching (AIM) model states that infants code human acts within an innate supramodal system that unifies observation and execution of motor acts (Meltzoff & Moore, 1997). Such a system may be similar to the notion of body schema. The posterior parietal cortex would then be of critical importance for this theory.
- The kinesthetic–visual matching requires some kinesthetic involvement in visual experiences of bodies, including one's own and those of others (Mitchell, 1993). The left parietal cortex is a key neural component of that theory.
- The goal-directed theory suggests that children first decompose observed actions and then reproduce them according to a hierarchy of goals (Bekkering, Wohlschläger, & Gattis, 2000). This theory requires the mirror system and executive functions (attention, action parsing, working memory), and thus would predict prefrontal cortex participation in imitation.
- The associative sequence learning (ASL) suggests that imitation is experience based and consists of a set of bidirectional excitatory links between sensory and motor representations of movement units (Heyes, 2001). This theory is compatible with the mirror neuron account but also requires nonspecific imitation mechanisms that regulate intentional action. These mechanisms are likely to be subserved by the prefrontal cortex.
- Rogers and Pennington (1991) proposed that two macrocomponents are implicated in imitation: (1) cross-modal representation processes extract patterns of similarity between self and other, and (2) executive functions. Prefrontal cortex in conjunction with the parietal cortex are crucial neural systems for this theory.

*Note.* This list is not intended to be exhaustive but aims at showing the similarities and the differences between these different theories.

direct perception–action coupling mechanism, also called the mirror system. Such a system provides a key foundation for the building of imitative and mindreading competencies. However, additional computational mechanisms are necessary to account for their full maturation.

## PERCEPTION–ACTION COUPLING AND MOTOR REPRESENTATIONS

Imitation requires that one maps one's own behavior onto the behavior observed in another individual. Such a mapping between the demonstrator and the imitator is the functional bedrock of any form of social learning,

copying, or mimicry and supposes a correspondence between two agents. It also necessitates a coupling mechanism between perception and action. In fact, perception and action cycles constitute the fundamental base of the nervous system. 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 (Sperry, 1952). The metaphor of "affordance" was coined to account for the direct link between perception and action (Gibson, 1966). 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 trashing," but the affordances presented by a garbage can to a raccoon would be radically different. Then 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, Shepard makes explicit reference to internal representation, and makes it possible to articulate the notion of resonance with that of motor representations.

In addition, humans actively seek information about themselves and others. 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 or 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 the mental content related to the goal or the consequences of a given action and the covert neural operations that are supposed to occur before an action begins. There is no ontological reason to consider these two levels of description (i.e., mental and neural) as separate, and least of all independent from one another.

Today, the common coding 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 (Prinz, 1997). This theory states that perception of an action should activate action representations to the degree that the perceived and the represented action are similar (see Knoblich & Flach, 2003, for empirical evidence).

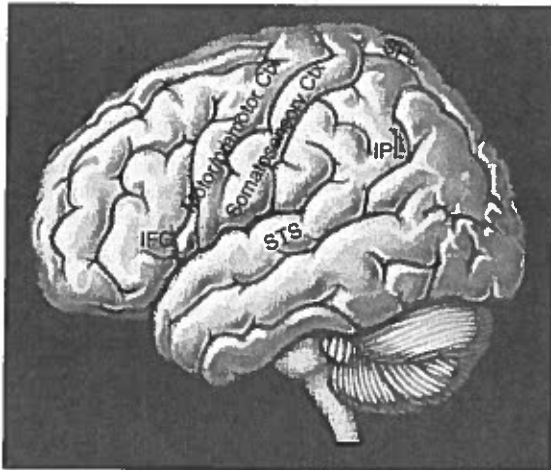
The discovery of "mirror neurons" in the ventral premotor cortex (F5 region) of the macaque monkey that fire both when it carries out a goal-directed action and when it observes the same action performed by another individual (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996) provided the first convincing physiological evidence for a direct matching between action perception and action representation. More recently, it was found that a subset of these mirror neurons also respond 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 (Umiltà et al., 2001). Therefore, specific neurons in this region respond to the representation of an action rather than to the action itself. Ongoing work by this laboratory extended this idea by showing that some neurons display mirror properties between motor and other modalities such as audition (Kohler et al., 2002). 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, Fogassi, Fadiga, & Rizzolatti, 2002). In a recent study, Raos, Evangeliou, and Savaki (2004) used the quantitative [ $^{14}\text{C}$ ]deoxyglucose method (a quantitative autoradiographic method used to map very precisely the spatial distribution of metabolic activity) in monkeys that either grasped three-dimensional objects or observed the same movements executed by humans. They found that the forelimb regions of the primary motor cortex (MI) and the primary somatosensory (SI) cortex were significantly activated in both cases. This study provides strong evidence for use of MI representations during the observation of actions by demonstrating that the observation of an action is represented in the primary motor and somatosensory cortices as is its execution. It also indicates 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. These findings support the direct-matching hypothesis that holds that one understands actions when one maps the visual representation of the perceived action onto one's own motor representation of the same action.

Another cortical region that contains neurons responding to the observation of actions performed by others is located in the superior temporal sulcus (STS). In the macaque monkey, Perrett and colleagues (1989) have 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. 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 discharge also during the observation of goal-directed hand movements (Perrett, Mistlin, Harries, & Chitty, 1990). Moreover, a population of cells, located in the anterior part of the STS respond 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 et al., 2000). In addition, the responses of a subset of these cells are modulated by the direction of attention (indicated by 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 F5 neurons, STS neurons do not appear to be endowed with motor properties. It was 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 also activate circuits comprising mirror neurons, which can, in principle, reproduce the perceived action (Rizzolatti, Fogassi, & Gallese, 2001). The two areas, STS and F5, are not directly connected, but both of them are linked to the parietal lobule area, which projects to the premotor cortex (see Figure 11.1 for corresponding areas in the human brain).

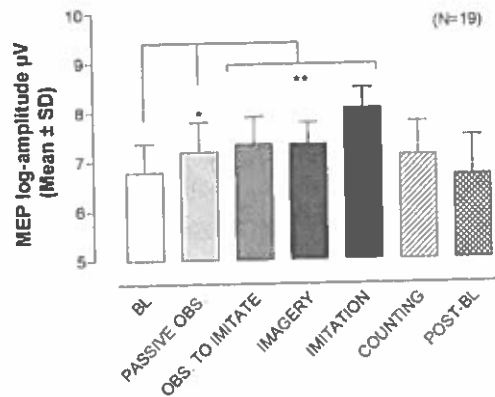
Evidence for a matching system between perception and action in humans continues to accumulate. For instance, it was found that when individuals observe a block-stacking task, the coordination between their gaze and the actor’s hand is predictive of the next action, rather than reactive to their last movement, and is highly similar to the gaze–hand coordination when they 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.



**FIGURE 11.1.** A lateral view of a human left hemisphere. IFG, inferior frontal gyrus; STS, superior temporal sulcus; IPL, inferior parietal lobule (Brodmann’s areas 39 and 40); SPL, superior parietal lobule (Brodmann’s areas 5 and 7). Note that the IFG corresponds to the ventral premotor cortex in monkeys in which area F5 is located. The premotor cortex has a central role in the selection of movements. Neurons in the posterior portion of the STS are triggered by the sight of actions performed by others. The SPL is involved in coding space and in directing spatial attention in relation to the control of body movements. The left IPL mediates motor representations, and the right IPL is critical for the sense of agency.

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 would be normally involved in the actual execution of the observed actions (Buccino et al., 2001). In another domain it has been found that speech listening is associated with an increase of motor-evoked potentials (MEP) 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). In another recent study, participants were asked to observe, imagine or imitate hand actions while transcranial magnetic stimulation (TMS) was delivered over their hand motor area of the left hemisphere (Clark, Tremblay, & St.-Marie, 2003). TMS generates magnetic field impulses, which stimulate underlying neurons in a focused volume and allow one to measure peripheral responses such as latencies and amplitudes. While the condition of imitation was the one to produce the greatest MEP, recorded in muscles of the dominant hand, there is significant response in both the observation and imagery conditions (Figure 11.2).

This perception–action matching system offers a parsimonious explanation of how we understand the actions of others, by a direct mapping of the visual representation of the observed action into our motor representation of the same action (Blakemore & Decety, 2001). This direct translation of perceived actions in others into motor output in oneself constitutes a shared rep-



**FIGURE 11.2.** Comparison of the mean changes in motor evoked potentials log—amplitude in a group of participants during various experimental conditions including passive observation, observation to imitate, mental imagery, and imitation of hand actions. BL, baseline. From Clark, Tremblay, and St. Marie (2003). Copyright 2003 by Pergamon Press. Reprinted by permission.

representational framework for self and other actions at both computational and neural levels (Decety & Sommerville, 2003). Furthermore, the fact that perception is itself tangled up with specific possibilities of action raises the idea that internal representations the mind uses to guide actions are best understood as action- and context-specific control structures rather than as passive recapitulations of external reality (Clark, 2001).

### FROM MOTOR PRIMING TO SOCIAL FACILITATION

One consequence of the functional equivalence between perception and action is that watching an action performed by another person facilitates the later reproduction of that action in oneself. For instance, a series of psychophysics studies demonstrated that when subjects are asked to produce gestures on cue, the response is quicker when stimulus and response gestures matched than when they were incongruent (Sturmer, Aschersleben, & Prinz, 2000). The response was also faster when subjects are asked to produce the response under imitative cueing than under symbolic cueing conditions (e.g., when shown a certain color). These findings also cast some light into "social facilitation," which accounts for the demonstration that the presence of other people can affect individual performance.

A series of experiments on spatial compatibility, based on reaction time, demonstrated that actions at the disposal of another agent are represented and have impact on one's own actions, even when the task at hand does not require taking the actions of another person into account (Sebanz, Knoblich, & Prinz, 2003). The authors used a spatial compatibility task distributed among two people so that each participant had control of one of two responses. Subjects were asked to press a key in response to a cue (e.g., color of a visual stimulus) while an irrelevant cue was simultaneously presented. The speed with which subjects produced the desired response was influenced by the direction of the arrow (irrelevant cue), a finding that can be explained if subjects were representing the actions of the other as if they were their own. These results show that one's own actions and others' actions are represented and planned in a functionally equivalent way. This mechanism also accounts for response facilitation (i.e., the automatic tendency to reproduce an observed movement, known as mimicry) (see Moody & McIntosh, Chapter 4, this volume) a type of imitative response. It is important to note that this behavior does not imply an understanding of the meaning of the imitated action (e.g., laughing and yawning). Copying the behavior of conspecifics (social learning) depends on the relative automaticity of some forms of imitation. It has an adaptive advantage for communication and social interaction (Chartrand & Bargh, 1999).

Another consequence of this perception-action matching mechanism is that stimuli that can be tied to the representation of one's own body should



be more imitable than those that cannot be mapped. In one experiment, Castiello, Lusher, Mari, Edwards, and Humphreys (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. They showed a priming advantage for the latter. A cerebral correlate of this effect seems to involve the premotor cortex and the right parietal cortex. Perani and colleagues (2001) reported greater activity in these regions when participants observed grasping movements executed by a human hand than when the same actions were performed by a virtual hand. Subsequent work by Castiello (2003) showed priming effects even when the kinematics of a model are not available and suggests that the motor intention of conspecifics can be inferred from their gaze. In a follow-up functional magnetic resonance imaging (fMRI) study, the same group demonstrated selective activation of the left premotor cortex when participants observed a human model performing grasping actions (Tai, Scherfler, Brooks, Sawamoto, & Castiello, 2004). This activation was not evident for the observation of similar actions performed by a robot.

A further argument in favor of the common mechanism for observed and executed action is provided by the study of Kilner, Paulignan, and Blakemore (2003) that showed interference effect, in the form of increased variance of movement, when subjects execute a movement while simultaneously observing someone else executing an incongruent movement. This interference occurred only when the incongruent movements were executed by another human agent, and not when they were performed by a robotic arm.

Another compelling demonstration of the involvement of motor representation 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 motion paradigm, originally developed by Shiffrar and Freyd (1990), to present participants in the scanner with a human model in different positions. Depending on the activation conditions, the 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 the subjects perceived possible paths of human movement (performed with a right limb). No activation in these areas was detected during conditions of impossible biomechanical movement paths.

Altogether these findings provide strong evidence that one represents one's own action and other's actions according to a similar neural and cognitive framework and fit neatly with the idea that we implicitly use our own motor representations system as a model to perceive and understand others. In addition, these data are consistent with developmental research, which has shown that our tendency to imitate reflects a consistent differentiation of animate and inanimate objects. For instance, a study indicates that young infants of ages 5–8 weeks imitate tongue protrusion openings of a human model but not when this gesture is performed by an object (Legerstee, 1991).

## IMITATION: FROM SIMPLE ACTS TO COMPLEX ACTIONS

Given the growing evidence for the direct perception–action coupling in the premotor/motor and posterior parietal cortices during action observation, it is likely that such a mechanism is at play during imitation. This direct mapping would at least partly account for the inborn ability to match seen movements of others with felt movements of their own (Meltzoff & Moore, 1977).

Some first evidence for the involvement of the mirror system during imitation of simple finger movements comes from an fMRI study conducted by Iacoboni and colleagues (1999). In that study, 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 homologue to F5 in the monkey), the right anterior parietal region, the right parietal operculum, and the right STS region.

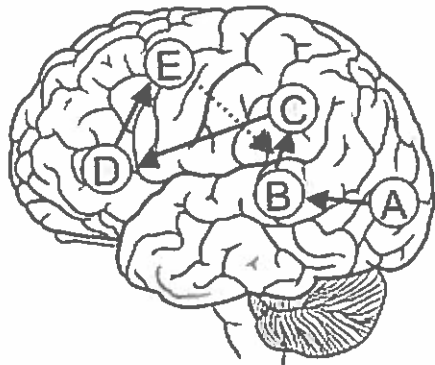
A series of neuroimaging studies demonstrated that the intention to imitate has a top-down effect on the brain regions involved in the observation of actions. In the scanner, participants were instructed to carefully watch pantomimed actions performed by a human model either for later recognition or for imitation (Decety et al., 1997; Grèzes, Costes, & Decety, 1998). When conditions of observation of action 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 (Plate 11.1). A different pattern of brain activation was found when subjects were observing the actions for recognition. In that case, the parahippocampal gyrus in the temporal lobe was chiefly activated. Thus the intention to imitate triggers additional information processing of executive functions that are necessary to hold in working memory the actions perceived, and also inhibitory mechanism to refrain imitating during the scanning.

Using magnetoencephalography (MEG), Nishitani and Hari (2000) investigated the cortical temporal dynamics of action representation during execution, online imitation, and observation of righthand reaching movements that ended with a precision pinch of the tip of a manipulandum. During execution, the left inferior frontal cortex was activated first (peak around 250 milliseconds [ms] before the pinching); this activation was followed within 100–200

ms by activation in the left primary motor area and 150–250 ms 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, neuromagnetic measures were taken in participants who observed still pictures of lip forms, online imitated them, or made similar forms in a self-paced manner (Nishitani & Hari, 2002). In all conditions and in both hemispheres, cortical activation progressed in 20–70 ms 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 ms later, to the primary motor cortex (see Figure 11.3). The signals of Broca's area and motor cortex were significantly stronger during imitation than other conditions. These results demonstrate that still pictures, only implying motion, can activate the human mirror neuron system in a well-defined temporal order.

In one recent study, Williams and colleagues (2006) compared a group of autistic individual to a control group in an imitation task (finger movements). Both groups performed the task well. In comparison with healthy subjects, they found reduced hemodynamic activity in brain areas involved in movement analysis (visual cortex, temporoparietal cortex) and integration of this



**FIGURE 11.3.** Schematic representation of the neural regions that constitute the basic neural architecture of imitation. (A) Visual cortex; (B) posterior STS; (C) rostral sector of the inferior parietal lobule; (D) inferior frontal gyrus; (E) motor cortex. The solid arrows indicate the assumed order of cortical activation measured by MEG (Nishitani & Hari, 2002). The dashed arrow represents the putative efferent copies of motor commands, which are used to predict the sensory consequences of the planned imitative behavior (see Decety, Chaminade, Grèzes, & Meltzoff, 2002; Iacoboni et al., 2001).

information into body knowledge (parietal cortex), action production, and mental state attribution (medial prefrontal cortex). Interestingly, this study did not reproduce the activation in Broca's region in the control group (see Table 11.2). The authors argued that the STS and inferior parietal cortex serve a self-other matching function between observed and executed actions by matching the intentions; it recognizes two different actions as similar even if they are achieved differently.

As described by Whiten (Chapter 10, this volume), action reproductions involving goals and means are dissociable (as seen in emulation) and therefore may partly tap distinct neural processes. Support for this hypothesis comes from a neuroimaging study that examined the neural instantiation of processing the goal and the means in an imitation paradigm (Chaminade, Meltzoff, & Decety, 2002). In this experiment, participants observed a human agent (only his hand and forearm were visible) building Duplo block constructions, and they were asked to observe and imitate either (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 subjects imitated either the goal or the means, suggesting that these regions are 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 (see Figure 11.4).

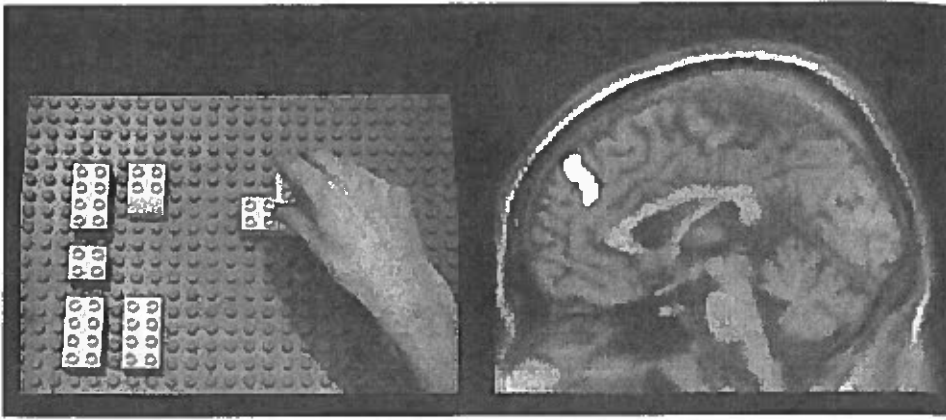
These findings support the idea that the means and the goal of imitation partially rely on dissociable circuits. Interestingly, the medial prefrontal region activation during imitation of the means indicates that observing the means used by another individual prompts the observer to construct/infer the goal toward which this 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 & Tanaka, 2004). This latter aspect is present in conditions of imitation of the means without knowing the final position of the action made by the model.

In a recent fMRI study, Buccino and colleagues (2004) addressed the issue of imitation of a new skill. Musically naïve individuals were scanned during four conditions: (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 consists of the inferior parietal lobule and the posterior of the

**TABLE 11.2. Questions for Future Directions**

Neuroimaging data help to answer fundamental questions about the mechanisms subserving imitation. However, their interpretation in relating structure to function should be done with caution. It is difficult to derive the computational function of an area without taking into account its extrinsic and intrinsic connectivity, the distribution of receptor types, and the information processing of the intrinsic neurons. Such information is generally lacking. In addition, a set of cortical areas may be active in a wide range of functions from action perception to theory of mind, but across those functions the networks in which they participate may be quite different (Cacioppo et al., 2003). In the domain of imitation, a number of specific questions need to be elucidated, including but not limited to:

- What is the role of Broca's region in action-perception coupling and imitation? While there is no dispute that in the monkey, neurons in F5 region code the goal of action and are involved in action understanding (Rizzolatti & Craighero, 2004), findings appear more diverse in humans. For instance, it has been demonstrated that the perception of auditory or visually presented temporal patterns involves area 44 (Schubotz & von Cramon, 2000), and that attention to the timing property of three consecutively presented visual objects (i.e., small circles) activates that region too (Schubotz & von Cramon, 2001). Broca's area participates in delayed execution and as such in movement preparation (Makuuchi, 2005). A recent fMRI experiment suggests that the left inferior frontal gyrus serves as a mechanism for general selection beyond that in semantic retrieval (Zhang, Feng, Fox, Gao, & Tan, 2004). It should, however, be noted that Broca's region contains motor representation of hand and mouth movements. It is thus logical to detect its activation in observation and imitation of hand and speech (e.g., Iacoboni et al., 2001).
- The posterior portion of the temporal cortex is an important component in a circuit involved in social cognition, which, through direct and indirect connections, receives input both from the ventral and the dorsal visual streams, the amygdala, the orbitofrontal cortex, and the prefrontal cortices. It seems that this region can be subdivided into different areas (in the right hemisphere), which may play distinct roles in the detection of agency and the representation of intentional actions (Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004).
- Which circuit mediates forward modeling? Activation of the superior parietal cortex, present when participants are instructed to observe action to imitate (e.g., Grèzes et al., 1998), may reflect backward projections of sensory copies of intended actions. A similar mechanism is thought to take place in the parietal operculum (Blakemore, Frith, & Wolpert, 1999), and in the STS (Iacoboni et al., 2001). The cerebellum is also considered to instantiate forward and inverse models (Wolpert, Miall, & Kawato, 1998).
- How is the motor resonance system functionally linked (and which anatomical pathways are involved) with theory of mind processes? Neuroimaging studies have revealed a system with three components: the medial prefrontal cortex, temporal poles, and posterior STS. This latter region is also found in action observation and thus may play a special role in linking the two systems. Importantly, the posterior STS has direct connections with the medial prefrontal cortex. Frith and Frith (2003) have proposed that this area is involved in detecting the behavior of agents, and analyzing the goals and outcomes of this behavior.



**FIGURE 11.4.** When participants observe, in order to imitate, another human agent building a Duplo construction (on the right) and when the goal of his actions is hidden, selective activation of the right medial prefrontal cortex was detected. This region is acknowledged to play a critical role in theory of mind. From Chaminade, Meltzoff, and Decety (2002). Copyright 2002 by Academic Press. Adapted by permission.

inferior frontal gyrus plus the adjacent premotor cortex (mirror neuron circuit). This circuit, known to be involved in action understanding, starts to be active during the observation of the guitar chords. During pause, the middle frontal gyrus (area 46) in addition to the structures involved in motor preparation (dorsal premotor cortex, superior parietal lobule, rostral mesial areas) also become active. The authors 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 with Brodmann's area 46 playing a fundamental orchestrating role.

### IMITATION AND EMOTION PROCESSING

The perception–action coupling mechanism may also apply (at least partly) to emotion processing. In this vein, the perception of facial expression of emotions (e.g., disgust) activates the neural mechanisms that are responsible for the generation of emotions. Such a system 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) (Adolphs, 2002). This is the facial feedback hypothesis as described by Moody and McIntosh

(Chapter 4, this volume). For example, while watching someone smile, the observer activates the same facial muscles involved in producing a smile at a subthreshold level, which creates the corresponding feeling of happiness in the observer. There is evidence for this mechanism in the recognition of emotion from facial expression. For instance, viewing facial expressions triggers expressions on one's own face, even in the absence of conscious recognition of the stimulus (e.g., Wallbott, 1991).

Making a facial expression generates changes in the autonomic nervous system and is associated with feeling the corresponding emotion). In a series of experiments, Levenson, Ekman, and Friesen (1990) instructed participants to produce facial configurations for anger, disgust, fear, happiness, sadness, and surprise while heart rate, skin conductance, finger temperature, and somatic activity were monitored. The authors found that such a voluntary facial activity produces significant levels of subjective experience of the associated emotions, as well as specific and reliable autonomic measures. In another study, Ekman and Davidson (1993) demonstrated similar patterns of electroencephalographic activity for spontaneous and voluntary forms of smiling. Recently, an fMRI experiment confirmed these results by showing that when participants are required to observe or to imitate facial expressions of various emotions, increased neurodynamic activity is detected in the STS, the anterior insula, and the amygdala, as well as areas of the premotor cortex corresponding to the facial representation (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003). In another study, participants were scanned while watching movies of facial expressions (smile or frown) and hand movements (move index or middle finger). The participants watched the movies under three different conditions: passive viewing, active imitation, and an active motor control. The authors found evidence for a common cortical imitation circuit for both face and hand imitation, consisting of Broca's area, bilateral dorsal and ventral premotor areas, right superior temporal sulcus, supplementary motor area, posterior temporo-occipital cortex, and cerebellar areas. For faces, passive viewing led to significant activation in the right ventral premotor area, whereas imitation produced bilateral activation (Leslie, Johnson-Frey, & Grafton, 2004).

The direct link between perception and action mediates the phenomenon of emotional contagion, defined as "the tendency to automatically mimic and synchronize facial expressions, vocalizations, postures, and movements with those of another person and consequently to converge emotionally" (Hatfield, Cacioppo, & Rapson, 1994). For instance, disgust is a strong negative emotion that, like fear, carries important survival cues for the self but also for the other who learns to avoid the ingestion of toxic aliments just by observing another conspecific's reaction. Phillips and colleagues (1997) have shown that normal volunteers presented with both strong and mild expressions of disgust activated anterior insular cortex but not the amygdala, and that strong disgust also activated structures linked to a limbic cortico-striatal-thalamic circuit. Another fMRI study extended these findings by showing that similar brain

networks were involved in both the recognition (watching video clips of facial expression) and the experience (inhaling odorants) of disgust (Wicker et al., 2003). The authors found that observing facial expressions and feeling disgust activated the same sites in the anterior insula and anterior cingulate cortex.

The capacity to copy facial expressions of others appears to originate in the prewired direct mapping between visually perceived faces of others and the motor system of the observer. This motor activity can drive the matching emotional response. Such a primitive sympathetic response, which is often subliminal, constitutes one important process involved in emotion sharing. However, while this mechanism may be necessary, it does not seem to be sufficient to support empathy (i.e., an affective response that stems from the perception and the understanding of another emotional state without confusion between self and other). It has been argued that without self–other awareness, executive function, and emotion regulation processing, there is no true empathy (see Decety & Jackson, 2004).

### THE ROLE OF INHIBITION

If one accepts that imitation is, to some degree, a prepotent response tendency such as in mimicry, it is, however, not an adaptive behavior in many everyday situations. Why then do we not imitate every behavior we encounter? 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 (e.g., Lhermitte, Pillon, & Serdaru, 1986). These authors 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 mesial 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 feeling compelled to use



objects (i.e., utilization behavior). This refinement of frontal–parietal mechanisms opens up new ways for not only 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 (Eslinger, 2002).

In that context, it is interesting to note that in healthy individuals, the right frontopolar cortex is reliably activated when they watched actions for later imitation (Decety et al., 1997; Grèzes et al., 1998), but not when they observed these actions for later recognition. Furthermore, this prefrontal activation was detected only for those actions that were in the motor repertoire of the subjects (e.g., meaningful actions) but not for meaningless actions. Moreover, when meaningless actions were learned by the participants a few days before the positron emission tomography (PET) exam, and thus became familiar, the frontopolar cortex was then engaged during observation with the intent to imitate (Grèzes, Costes, & Decety, 1999). Consistent with this view, Brass, Zysset, and von Cramon (2001) carried out an fMRI study to investigate the cortical mechanisms underlying the inhibition of imitative responses. Their experiment 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 the hemodynamic response during incongruent versus congruent trials revealed strong activation in the dorsolateral prefrontal cortex (middle frontal gyrus) and activation in the right frontopolar cortex. 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.

It is important to note that the prefrontal cortex, which appears to exert its functions mostly through inhibition, is not fully mature immediately after birth. While cytoarchitecture reaches full development before birth in human, the myelination of prefrontal connective fibers extends long after birth, until adolescence (Fuster, 1997). This lack of inhibition, or mild inhibition at the beginning of childhood, confers developmental benefits through imitation. Then, inhibitory mechanisms progressively develop, in parallel to cognitive abilities for which inhibition is a requisite. Without executive functions (including attention, self-regulation, and inhibition), one would be driven by impulsive acts or automatic responses to physiological needs or environmental stimuli.

## RECIPROCAL IMITATION AND THE SENSE OF AGENCY

Imitation in human beings is not restricted to mimicry or learning new skills. We also recognize when others are imitating us. Reciprocal imitation is an essential part of communicative exchanges and plays an important role in

developing shared feelings and shared motivational states with others (e.g., Hobson, 1989). Moreover, there is good evidence that reciprocal imitation plays a constitutive role in the early development of an implicit sense of self as a social agent (Rochat, 1999). The ability to recognize oneself as the agent of an action, thought, or desire (the sense of agency) is crucial for attributing a behavior to its proper agent and plays a pivotal role in the development of cognition. The distinction between self-generated actions and actions produced by others is a key function for self-recognition. Such tracking or monitoring mechanism is crucial in social interaction in general and in reciprocal imitation in particular.

A number of functional imaging studies have pointed out the involvement of the right inferior parietal lobule in the process of attribution of an action to its proper agent. Such a process 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 subjects 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 also requested to perform the task, but they were aware that action seen on the screen was driven by the experimenter. 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.

One functional imaging study explored the extent to which being imitated and imitating the other relies on similar or distinct underlying neural mechanisms (e.g., Chaminade & Decety, 2002). In that study, participants were scanned while they imitated an experimenter performing constructions with small objects and while the experimenter imitated them (Decety, Chaminade, Grèzes, & Meltzoff, 2002). Results showed that a network of regions were commonly involved in the two reciprocal imitation conditions in comparison to a baseline condition (self-action). This network included the inferior frontal gyrus, left inferior parietal lobule, the superior frontal gyrus, the STS, the pre-SMA, and the right medial frontal cortex. In the condition in which participants imitated the other, increased activity was detected in the left inferior parietal cortex. This result is consistent with neuropsychological observations (e.g., Halsband et al., 2001), as well as functional imaging studies that have pointed out the systematic implication of the left parietal cortex in imitation (e.g., Chaminade, Meltzoff, & Decety, 2005; Makuuchi, in press; Tanaka & Inui, 2002; Williams et al., 2006). When participants' actions were imitated, additional activity was detected in the right inferior parietal cortex (see Plate 11.2).

The right inferior parietal lobule in reciprocal imitation can be explained with regard to its role in agency. Making agency judgments about who has performed an action is likely to be made on the basis of central representa-

tions coded in allocentric coordinates (Jeannerod, 1999). A common coding system of this kind is needed when being imitated by the other, because it is not possible to represent the actions of others in the egocentric coordinates used for generating our own actions. There is strong physiological evidence that the inferior parietal cortex implements this kind of remapping process that would be needed to generate representations of body movements in allocentric coordinates.

Interestingly, the mechanism that accounts for the correct attribution of actions and thoughts to their respective agents is also 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 (self) or from the third-person perspective (other). 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.

Further evidence for the role of the right inferior parietal cortex in the sense of agency is provided by neuropsychological studies in humans. For instance, Blanke, Ortigue, Landis, and Seeck (2002) have shown that direct cortical stimulation of this region in neurological patients induced out-of-body experience (i.e., the experience of dissociation of self from the body). 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, or somatoparaphrenia (Berlucchi & Aglioti, 1997).

## CONCLUSION

Taken together, the neurophysiological data reviewed in this chapter suggest that the basic circuit underlying imitation coincides with that which is active during action observation. This direct mapping of the observed action and its motor representation is mediated in the premotor cortex and the posterior parietal cortex. Such a mechanism (when not inhibited) is sufficient to explain motor mimicry and social facilitation. A similar mechanism is involved in emotion contagion, which is considered as an important precursor to the development of empathy. Thus, this basic mechanism accounts for continuity between all sorts of imitation. However, additional cognitive and neural mechanisms are required to fully account for human imitative capabilities, which extend beyond a simple motor resonance between self and other. For instance, the right inferior parietal cortex, in conjunction with the prefrontal cortex, play a critical role in the sense of agency and self–other correspondence. This is very important given the link between imitation, theory of mind ability, and empathy (see Rogers, 1999). The fact that children represent the

behavior of others in a psychological framework involving goals and intended acts, instead of purely physical movements or motions, and that they are capable of rational imitation, constitutes compelling demonstrations for such a functional link. Hence, some complex forms of imitation are also dependent on the attribution of intentions for which the medial prefrontal cortex and posterior temporal cortex (at the junction with the parietal cortex) are essential. Such a view is consistent with the idea that imitation is a precursor to full theory of mind, but the two capacities are not totally overlapping (Meltzoff & Decety, 2003; Rogers & Pennington, 1991; Williams, Whiten, Suddendorf, & Perrett, 2001) and may thus be implemented by different systems.

Future research is needed to elucidate the functional relation between the mirror system, executive functions, and mentalizing process and how they can be fragmented into subcomponents with their respective neural implementation (see Table 11.2 on page 263).

In addition, the identification of a network of brain regions involved in imitation does not fully inform us which areas (or nodes) are critical for the imitation function. Neuroimaging findings must therefore be complemented by lesion studies in neurological patients to better understand the computational role of each area within the network. Finally, functional neuroimaging studies with people who are impaired in imitation, such as those affected by autistic spectrum disorders are also desirable to cast some light on the neural and cognitive mechanisms that subserves imitation (see Williams & Waiter, Chapter 15, this volume).

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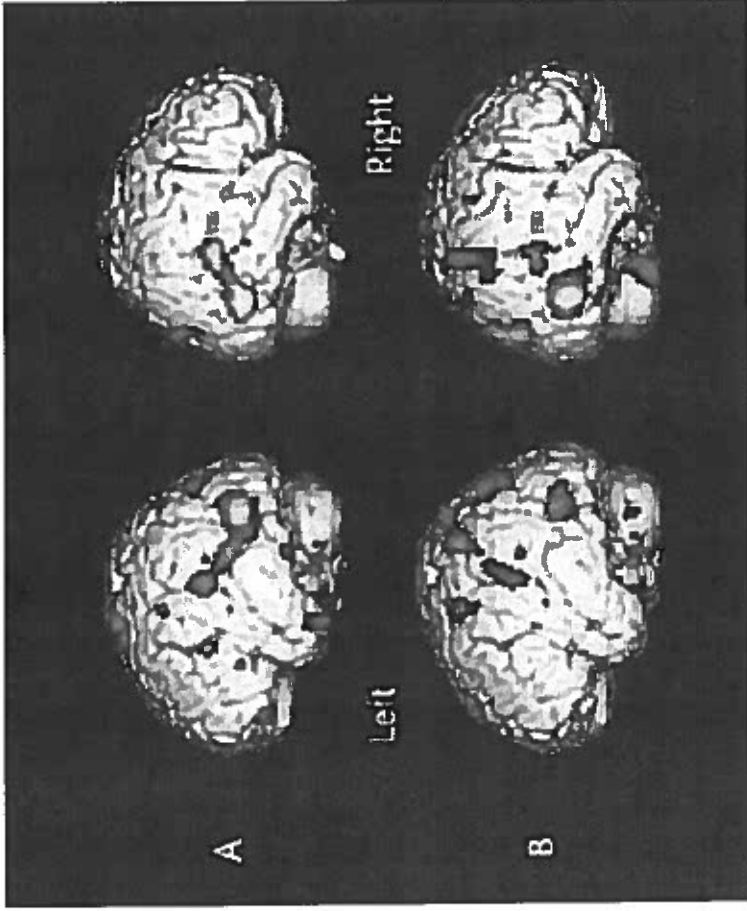
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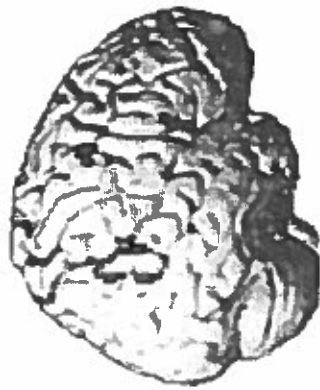
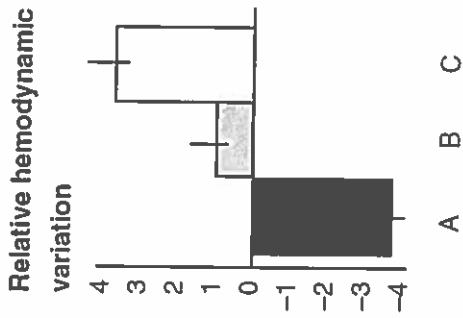
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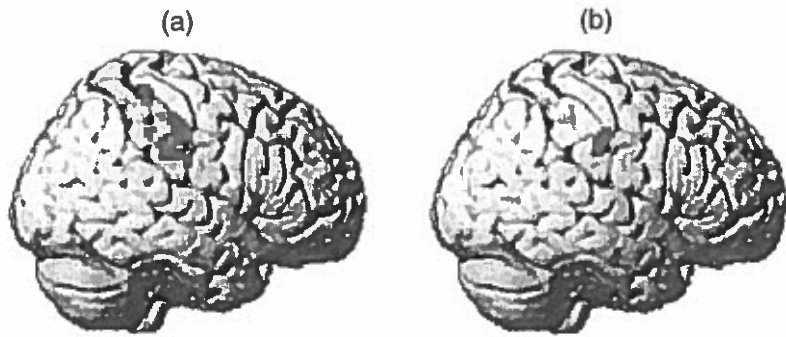




**PLATE 11.1.** Neurohemodynamic changes in a group of individuals who observed videoclips depicting meaningful right upper limb pantomimes executed by a human model with no specific task (A), and during the observation of similar stimuli with the intention to imitate them at the end of the scanning session (B). These two conditions are contrasted with the observation of static hand postures. Regions in which significant activation occurred during the perception of actions (Condition A) include the premotor cortex, Broca's area, STS, and left parietal cortex. The intention to imitate (Condition B) is associated with increase of hemodynamic activity in the supplementary motor area, the right premotor, and right parietal cortex. From Grèzes, Costes, and Decety (1998). Copyright 1998 by Psychology Press. Adapted by permission.



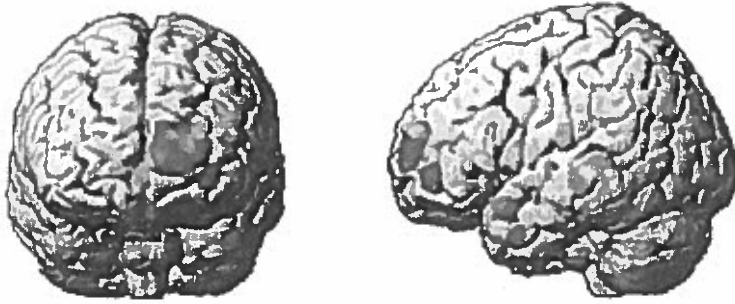
**PLATE 11.2.** Right inferior parietal lobule activation at the junction of the temporal cortex superimposed on a rendered MRI. In this study, participants were scanned during a variety of object-directed actions with small objects, including self-action (A), imitation of actions performed by an experimenter (B), and observation of their actions being imitated by the experimenter (C). Note the dramatic increase in this region in this latter condition. This region plays a pivotal role in the sense of agency. From Decety, Chaminade, Grèzes, and Meltzoff (2002). Copyright 2002 by Academic Press. Adapted by permission.



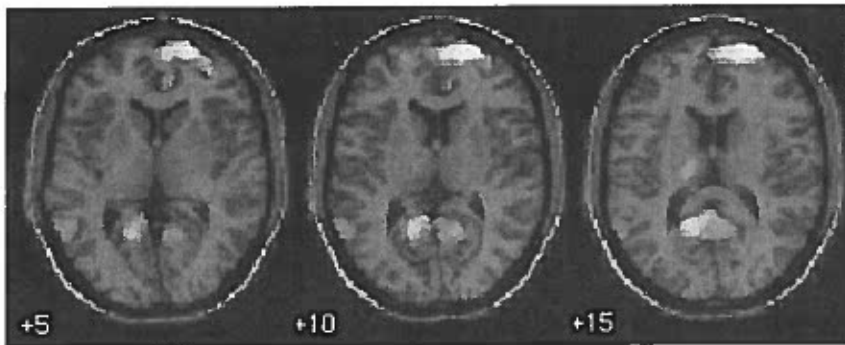
**PLATE 15.1.** Imitation versus [average of spatial cue execution + symbolic cue execution] masked to include frontal and parietal regions only. Random-effects analysis, threshold at  $p < .001$  uncorrected. (a) Controls; (b) group with ASD.



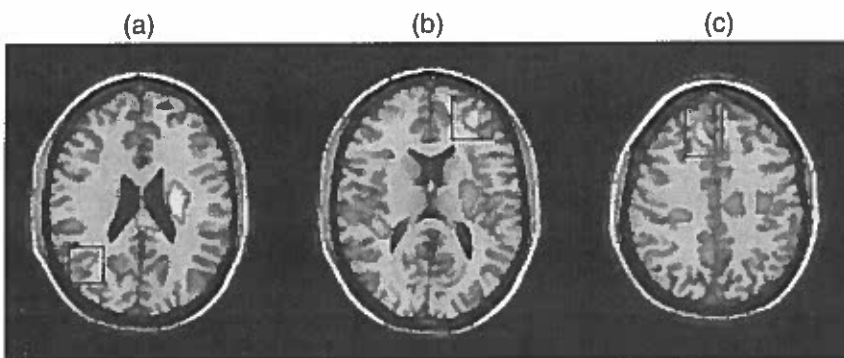
**PLATE 15.2.** Results of the two main contrasts rendered onto a single, semi-transparent, standard three-dimensional structural MRI image. Activation related to joint attention versus rest is in red; that due to non-joint attention versus rest is in green. Overlap is in yellow. Threshold at  $p < .001$  uncorrected.



**PLATE 15.3.** Results of two separate studies rendered onto a single three-dimensional standard structural MRI image. Areas where activation during joint attention is greater than during non-joint attention in this study are in green. Areas involving a separate group of individuals from Waiter et al. (2004), where gray matter volume in ASD was increased relative to controls, are in red. Areas of overlap are yellow.



**PLATE 15.4.** Sagittal sections of the brain showing areas of gray matter increase in ventral temporal cortex, left superior frontal gyrus, and right temporoparietal regions particularly. The blue area shows decrease in thalamic gray matter volume. The left side of the figure represents the right side of the brain.



**PLATE 15.5.** Sagittal sections of the brain showing reduced white matter volume in ASD compared to controls. (a) Left middle temporal; (b) right middle frontal; (c) left superior frontal regions. The left side of the figure represents the left side of the brain.