

4 The Neurophysiology of Imitation and Intersubjectivity

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4.1 Introduction

The purpose of this chapter is to marshal relevant findings from functional neuroimaging experiments on the relations between action and perception and on imitative behavior in humans in order to take a tentative step toward a better understanding of intersubjectivity. By “intersubjectivity,” we mean the process by which mental activity (motives, intentions, feelings, emotions) is transferred between the self and others’ minds (Trevvarthen, 1999). This process exists, since we possess the ability to conceive as mentalistic agents not just the self but also others, even though we have access only to their surface behavior. Subjectively private mental states are communicated via body movements (e.g., gaze, speech, facial expressions, or posture), which are the signs of intentionality.

We will argue that at a low level, intersubjective behavior and social cognition involve an automatic and unconscious motor resonance mechanism that relies on the physiological properties of the nervous system. There is substantial neurophysiological evidence, both in monkeys (Rizzolatti et al., 2001) and in humans (Blakemore & Decety, 2001), for a distributed set of brain areas (or clusters of neurons) that are active when actions are self-generated or observed. Although such a mechanism is necessary, we claim it is not sufficient to explain how the intentions behind bodily motions are understood, nor can it account for the sense of agency. Investigating imitation at the neural level can provide essential clues for understanding how the self and the others share intentions through social interactions. As several developmental psychologists have argued, imitation is a natural avenue to developing intersubjective transactions between the self and other selves (Meltzoff & Moore, 1995; Nadel & Butterworth, 1999; Tomasello, 1999; Trevvarthen, 1979).

Developmental research has indeed shown that babies are born with the capacity and the motivation to imitate human gestures, but that they are also equipped with what Meltzoff and Moore (1998) have termed a "like me" mechanism or a sense of like-meness. This mechanism gives human infants a way to discover that others are similar to themselves. Imitation of human actions is the first bridge between the infant and others, and it serves the dual function of differentiating the broad class of "others" into individuals and providing an early means of communicating with them. It is through mutually imitative games that infants progress from conceptions of others as entities with whom one can share actions to persons with whom one can share goals and intentions. In addition, a growing body of research demonstrates that early on, infants develop a sense of themselves as situated, differentiated agents in an environment, as well as a sense of themselves as communicative and reciprocating social agents (Rochat & Striano, 2000).

Even though there exist precursors of intersubjective behavior in the animal kingdom—for instance, the contagion of emotions (for empathy) and motor mimicry (for imitation)—in this chapter we consider these issues only in light of research carried out in human beings. Human social evolution has its roots in the natural history of the hominoid family, which diverged around 25 million years ago. It may be assumed that all behavior in primates, including our own species, derives from a combination of evolved tendencies, environmental modification, development, learning, and cognition (de Waal, 2001b). But continuity does not mean identity.¹ However, intersubjectivity has evolved to a special extent and has given rise to psychological processes described in terms of empathy, identification, or projection that are unique to humans, perhaps because of their relation to self-awareness. Imitation, like self-consciousness, may even be a distinctive aspect of human nature.

Self-consciousness could be regarded as just another adaptive trait, yet it has a great effect on our mental life. Not only are we capable of understanding and predicting our own and others' behavior, we have the ability to explain what our brain does and effortlessly make inferences about our own mental states and those of others. We have an idea of ourselves as

1. We take seriously the claim made by Povinelli and collaborators that evolution is real and that it produces diversity. Therefore it may be wrong to systematically assert that the parsimonious explanation of the behavioral similarities between humans and chimpanzees is the operation of equally similar psychological systems (see especially Povinelli & Bering, 2002).

agents; our awareness of causing an action is associated with a strong sense of self (S. Gallagher, 2000). Because we are self-conscious organisms, we explain our own behavior in terms of emotion, desires, intentions, and beliefs, and we assume that others also have similar mental states. In short, we have evolved from being behaviorists to being natural psychologists.

Humphrey (1980, 1982) long ago proposed that once self-consciousness had provided our species with a way of making introspective sense of our own behavior, then our own experiences and ways of understanding behavior would immediately and naturally be projected onto other people. Thus, humans come to understand the intentions of others through an introspective examination of their own mental states and processes—a kind of simulation of what it must be like to be in the "mental shoes" of the other person (Goldman, 2002; Harris, 2000; Gordon, 1986).

It is not satisfactory to talk about a set of areas activated when a specific action is performed without having a clear prior conception of both the processes involved and the expected brain responses.² Hence the search for understanding the functional architecture that implements intersubjectivity cannot proceed without careful definition of the relevant concepts (i.e., resonance, simulation, shared representations, imitation, and agency) that are used throughout this chapter. All of these concepts are rooted in the psychology and philosophy of mind and have come to be used only relatively recently in neuroscience.

The notion of *resonance* was introduced by Gibson (1966) as part of his ecological approach to perception, which assumes that: (1) perception serves an adaptive function and the external world must therefore provide information to guide biologically and socially functional behaviors; (2) this

2. As cognitive neuroscientists, we are well aware that powerful technologies such as positron emission tomography (PET), functional magnetic resonance imaging (fMRI), or magnetoencephalography (MEG) do not localize cognitive functions, but merely tell us where in the brain neurohemodynamic or electrically related activity takes place in relation to a given experimental paradigm. Having said that, we think that imaging techniques do contribute to revealing the functional architecture that instantiates the mechanisms involved in intersubjectivity. These neurophysiological data are especially worthy of consideration when they are integrated with data from other supplementary sources, such as developmental science, clinical neuropsychology, and psychopathology. In addition, the interpretation of neuroimaging data is probably more complex than behavioral data. One needs to be concerned not only with the nature of the task itself but also with the underlying physiology. For instance, it is not yet clear whether regional cerebral blood flow increases in PET or whether BOLD changes in fMRI reflect excitation or inhibition at the cellular level.

information is typically revealed in objective, physical, dynamic, multimodal events, as opposed to static, unimodal displays; (3) the information available in events specifies which events provided by environmental entities are opportunities for acting or being acted upon; (4) perception of these affordances depends upon the perceivers' attunements, that is, the particular stimulus invariants to which the perceiver attends. Resonance involves a simultaneous querying of many mechanisms at once and in parallel, just as a vibrating tuning fork can query many strings about their resonant frequencies at the same time. The idea requires both parallel processing, a radically modern idea in Gibson's time, and a group of mechanisms with which to resonate.

Later, Shepard (1984) proposed 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. It is interesting that Shepard proposed that the external constraints that have been most invariant throughout evolution have become most deeply internalized, and even in the complete absence of external information, the system can be excited entirely from within (while dreaming, for example). Thus, unlike Gibson, Shepard makes explicit reference to internal representation.

Today, the concept of motor resonance is used in neuroscience as a metaphor to describe the behavior of a neuron that fires both when a monkey performs a given action (such as grasping a peanut) and when it watches another individual performing the same action (Rizzolatti et al., 2001), or when similar premotor areas are found to be activated during the execution of a given movement as well as during the observation of the same movement performed by another person (Fadiga et al., 1995).

The notion of *shared representations* is widely used in social psychology, especially in the field of communication. For successful communication to take place, the speaker and the listener have to attribute similar meanings to representations of the topic of communication. Communicators establish a shared representation of the topic of conversation in the communication process (Krauss & Fussell, 1991). Research in social sciences suggests that communication leads to internalization of shared representations. More generally, the meaning of a given object, action, or social situation may be common to several individuals and thus should activate the same neural network in their respective brains. These shared representations constitute the contents of a culture (Bruner, 1990). Within a culture, shared beliefs unify the cognitive and motivational processes.

The notion of shared representations can be applied not just across different individuals but also within individuals. It is central to several cognitive models of intentionality. For instance, Gopnik (1993) argued that the same representational form is used to encode an embedded intentional relation whether the latter involves the self as agent or another agent. Another influential cognitive developmental model proposes that the monitoring of first-person information (i.e., self-generated signals) and third-person information (i.e., signals from visual perception), both of which are crucial to the normal adult's understanding of social cognition and intersubjectivity, activate an internal intentional schema (Barresi & Moore, 1996). This schema has the capacity to coordinate first-person and third-person information and compute the attribution of action to the self or to the other.

Moreover, there is a long-standing position in psychology which assumes that perception and action share common coding mechanisms (e.g., Viviani, 2002). Notably, the common-coding hypothesis (W. Prinz, 1997a; Hommel et al., 2001; Knoblich & Flach, 2001) states that actions are coded in terms of the perceivable effects they should generate, and assumes that the representations of the intended effects of an action determine the production and perception of an action. Thus perceiving events produced by other individuals should activate the same representational structures that govern one's own planning and control of these actions. Recently the concept of such shared representations has been used to account for the demonstration that similar brain areas are activated during mental representation of one's own action, mental representation of another's action, and observation of another's action (Decety & Grèzes, 1999; Jeannerod, 1999; Grèzes & Decety, 2001; Decety, 2002a; Decety & Sommerville, 2003).

Imitation is an innate (i.e., present at birth and prior to the experience of learning a particular association between a stimulus and a response) capacity in the human species; it is both effortful and intentional (Meltzoff & Moore, 1999a; see Heyes, vol. 1, ch. 6 and Anisfeld, vol. 2, ch. 4, for a different view). There are evolutionary precursors of imitation in other species but, as argued by R. Byrne and Russon (1998), most of the cases currently claimed to be animal imitation should be rejected in favor of a simpler explanation, such as response facilitation. Conversely, some copying by great apes that has been discounted as emulation may warrant reevaluation as imitation. Here we use a narrow conception of imitation which requires the learning of a novel action and copying of both the goal of the action and

the means used to achieve. In the studies described in this chapter, behaviors will be qualified as imitation if and only if they meet the following two criteria: the similarity of the goal and the means to achieve it and the novelty of each trial for the imitator.

4.2 Observing Actions Performed by Others

Although there is a large body of experimental data that have been interpreted in favor of the common coding of perception and action (W. Prinz, 1997a; Viviani, 2002), it is only in the past 15 years that neurophysiological evidence has started to accumulate (Decety & Grèzes, 1999). The discovery of mirror neurons in monkeys, which discharge during the execution of purposeful, goal-directed hand movements as well as when the monkey observes similar hand actions (Rizzolatti et al., 1996a; Rizzolatti, vol. 1, ch. 1), has encouraged the search for a comparable mechanism in humans.

Fadiga et al. (1995) recorded motor-evoked potentials elicited by transcranial magnetic stimulation (TMS) in subjects asked to observe grasping movements performed by an experimenter. At the end of the observation period, TMS was applied to the subject's motor cortex, and motor-evoked potentials were recorded from intrinsic and extrinsic hand muscles. The pattern of muscular response to this stimulus was found to be selectively increased in comparison with control conditions, demonstrating increased activity in the motor system during the observation of actions. This finding was confirmed by neuromagnetic measures made with magnetoencephalography (MEG) over the premotor cortex while the subjects observed another person manipulating an object (Hari et al., 1998). Similarities in electroencephalograph (EEG) signal desynchronization over the motor cortex were found to occur during both execution and observation of finger movements (Cochin et al., 1999). There are thus good arguments for low-level motor resonance phenomena, given that the motor cortex is activated during the observation of actions.

Several positron emission tomography (PET) studies have shown recruitment of premotor, parietal, and temporal activation during observation of actions. In the experiment by Rizzolatti et al. (1996b), the subjects were requested to observe the movements of an experimenter who grasped common objects. In another condition, the subjects had to reach and grasp the same object. Significant activation was detected in the left middle temporal gyrus and in the left inferior frontal gyrus. Another PET study con-

ducted by the same group found activation in the SMA proper, the inferior parietal cortex, and the inferior frontal gyrus on the left side (Grafton et al., 1996). Recently, a functional magnetic resonance imaging (fMRI) study also demonstrated that observation of an action activates the premotor cortex in a somatotopic manner, which is reminiscent of the classical motor cortex homunculus (Buccino et al., 2001).

A series of studies performed by our group manipulated the cognitive strategy of subjects who were watching hand actions by instructing them to memorize the action either for later imitation or for recognition (Decety et al., 1997; Grèzes et al., 1998, 1999). When the subjects observed actions for later imitation compared with passive observation of the same actions, a specific hemodynamic increase was detected in the 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 the subjects were observing the actions for recognition. In that case, the parahippocampal gyrus in the temporal lobe was activated. The intention to imitate thus has a top-down effect on the information processing involved in action observation. Observing the other in order to imitate tunes the regions involved in generation of action to a step beyond simple motor resonance, i.e., motor preparation. Note that in all of these studies, the right inferior parietal cortex was consistently found to be activated in conditions involving later imitation.

Altogether, these studies strongly support the view that action observation involves neural regions similar to those engaged during actual action production. Moreover, this motor resonance phenomenon seems to be selectively triggered by actions that belong to the motor repertoire of the subject watching them. J. Stevens et al. (2000) adapted the apparent motion paradigm, originally developed by Shiffrar and Freyd (1990), to present subjects in the PET 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. No selective activation of these areas was found during conditions of impossible biomechanical movement paths. These results are consistent with the notion that we may understand the actions of others in terms of our own motor system (Shiffrar & Pinto, 2002; Viviani, 2002). It is also interesting that no premotor or inferior parietal activation was detected when individuals were presented with goal-directed movement in

a virtual reality system (Decety et al., 1994). This may have been due to the poor resolution of the virtual reality system, which made it difficult for the subjects to perceive the movements as natural—that is, as produced by another biological agent—and hence to identify with the movements.

Such covert identification is critical. The capacity to identify with other conspecifics, considered a prerequisite to feeling sympathy and empathy (Hobson, 1989, 2002; Tomasello, 1999; Decety, 2002b), is a distinctive characteristic of human beings that other primates may not possess. New-born human beings are innately highly attuned to other people and motivated to identify with others. From the earliest months of life, infants are engaged with other people and with the actions and feelings expressed through other people's bodies (Hobson, 2002; Rochat, 2002). Developmental studies have shown that children can infer intentions from movements when they are performed by people, but not by mechanical devices (Legerstee, 1991; Meltzoff, 1995). Consistent with these observations, experiments that examined motor priming effects on imitation resulting from observation of a biological (human) versus a nonbiological effector system (a robot) have shown only the former to induce such effects (Castiello et al., 2002).

To test the hypothesis that only the perception of naturalistic actions maps onto existing representations of action, Perani et al. (2001) presented subjects with object-grasping actions performed either by a real hand or by means of 3-D virtual reality or a 2-D television screen. The results showed common activation foci, in the left posterior parietal cortex and in the premotor cortex, for observation of real-hand actions and artificial ones, with a greater increase in signal for the real-hand condition. A striking finding was the selective involvement of the right inferior parietal cortex and the right superior temporal gyrus (STG) only in the condition of watching a real human hand grasping the objects.

Thus we propose in this chapter not only that the human system involved in the perception and understanding of actions performed by other selves might be based on a direct neural matching mechanism for perception and action, but also that it requires the capacity to both identify with other selves and to distinguish the self from other selves. We believe that such mechanisms are necessary to experience intersubjectivity and empathy. After all, as Hodges and Klein (2001) remind us, what makes humans special is their meta-ability—that is to say, their ability to go up a level and see the self and other as two distinct members in the category of agents.

4.3 Representing the Actions of Oneself versus Those of Others

One of the distinctive capacities of human beings resides in self-consciousness, which provides us with a way of consciously representing the intentions and actions of ourselves and others (Povinelli & Prince, 1998). Hence, we can ask human subjects to mentally simulate an action and simultaneously explore the underlying neural substrate thus activated. Psychophysics experiments have shown that temporal and cinematic properties of mentally represented actions mimic those of the real events represented (for a review see Viviani, 2002). For instance, in an experiment conducted by Parsons (1994), the subjects were shown pictures of either the left or the right hand in different orientations. In one condition, the task was to reproduce the position being shown by actual movement of the appropriate hand. In the second condition, no overt movement was required; the subjects simply had to tell whether the stimulus was a right or a left hand. In both conditions, the response times varied linearly as a function of the orientation of the hand and were highly correlated.

The similar constraints on actually performed and mentally simulated actions that act on internal representations may be hypothesized to reflect their neurophysiological instantiation. This idea is validated by several neuroimaging studies that have found activation sites in the SMA, premotor, primary motor, inferior frontal, and inferior parietal cortices lateralized to the left hemisphere, as well as the ipsilateral cerebellar cortex when subjects imagine right-hand-related actions (Decety et al., 1994; Lang et al., 1994; Stephan et al., 1995; Grafton et al., 1996; Roth et al., 1996; Porro et al., 1996; Parsons & Fox, 1998). Thus, consciously representing an action involves a pattern of brain activation that resembles that of an intentionally executed action because all of these areas are known to participate in action execution (Decety & Ingvar, 1990). There are differences, however, between actual and mentally represented actions in the SMA and in the cerebellum. It has been proposed that posterior cerebellar activation accounts for inhibition of movement during imagination (R. Lotze et al., 1999). This set of cortical areas, activated during both the generation and the mental simulation of one's own actions, can be described as sustaining the neural representation of actions and account for their functional equivalence.

Recently, Ruby and Decety (2001) asked subjects to imagine an action as being performed either by themselves (first-person perspective) or by

another individual (third-person perspective). Both subjective perspectives were associated with common activated clusters in the SMA, the precentral gyrus, and the precuneus. First-person perspective-taking was specifically associated with increased activity in the left inferior parietal lobule and the left somatosensory cortex, whereas the third-person perspective recruited the right inferior parietal lobule, the posterior cingulate, and the frontopolar cortex.

A similar pattern of activation was discovered in a follow-up study that investigated perspective-taking at the conceptual level (Ruby & Decety, 2003). In this study, the participants, who were selected exclusively from among medical school students, were asked to judge the truthfulness of affirmative health-related sentences, from either their own perspective or that of laypersons. The left inferior parietal lobule was involved in a first-person perspective, while the frontopolar cortex and the right inferior parietal lobule were strongly activated when the subjects took the third-person perspective.

These results support the notion of shared representations of self and other, since common activated areas are found in both subjective perspectives, even at the conceptual level. However, the results also point out the crucial role of the inferior parietal cortex (and the frontopolar cortex) in distinguishing the perspective of the self from that of others, as well as the involvement of the inferior parietal cortex in intersubjectivity.

4.4 Reading Others' Intentions and Emotions

Developmental research indicates that the distinction between matching an observed motor program (the means of the model) and reproducing the correct use of an object (the goal) is deeply rooted in human cognition. For example, even 18-month-old children have no difficulty in distinguishing the surface behavior of people (what they actually do, the means) from another deeper level (what they intend to do, the goal) as demonstrated by Meltzoff (1995) using a reenactment procedure. This supports the idea that when observing someone's action, the underlying intention is equally or perhaps more important than the surface behavior itself (Baldwin & Baird, 2001).

A neuroimaging experiment was designed to differentiate the neural correlates of two implicit ways of retrieving an action, either by observation of its means or by referring to its goal (Chaminade et al., 2002). Although there is no clear-cut division in ecological situations (Whiten & Ham, 1992), the goal in this experiment was operationalized as the end state

of manipulating the object and the means as the motor program used to achieve this relation. The actions consisted of sequentially moving Lego blocks from a starting position to a specific place in a Lego construction being built. The experimental conditions were derived from a factorial design in which the factors were (1) what was shown to the subjects during observation of the model, which, depending on the conditions, could be the whole action, only the means, or only the goal; and (2) the response performed by the subject, which could be to imitate, to observe, or to act freely. The results revealed partially overlapping clusters of increased regional cerebral blood flow (rCBF) in the right dorsolateral prefrontal area and in the cerebellum when the subjects imitated either the goal or the means. Moreover, specific activity was detected in the medial prefrontal cortex during the copying of the *means*, whereas copying the *goal* was associated with increased activity in the left premotor cortex.

Our results suggest that for normally functioning adults, imitating a gesture activates neural processing of the intention underlying the observed action. Activity in these frontal areas reflects the transformation of the partial information about an action given by the model into a complete action to be performed by the subject. The finding of the involvement of the right dorsolateral prefrontal cortex fits with its critical role in the preparation of forthcoming action based on stored information (Pochon et al., 2001). This region was more activated during the interaction that described the copying of the goal, which leads us to suggest that it stores the representation of the goal in short-term working memory. Therefore its activation during copying of the means suggests that this condition also activates a representation of the goal that is built online from the observed gesture (Miller, 2000). The right medial prefrontal cortex, which is known to play a critical role in reading others' intentions (Happé et al., 1999; Blakemore & Decety, 2001), was only found to be activated by the copying of the means, and may reflect the retrieval of the goal or intention of the actor from the observation of his or her gestures.

A powerful way to demonstrate the neural representation of the internal coupling between production, perception, and understanding postulated by the motor resonance theory as expressed by Shepard (1984) is to exploit the anticipatory effects of motor competence. Anticipatory adjustments are present in many language-related movements, such as speech, typing, and handwriting, and also in pointing (Viviani, 2002). This is particularly interesting because subjects are not conscious of these phenomena. For instance, in handwriting, anticipatory adjustments are used to predict the letter that is about to be traced (Orliaguet et al., 1997).

We designed a neuroimaging study in which an extremely simplified depiction of human motion was presented to the subjects. All activation conditions included a black dot moving on a white screen showing different trajectories (Chaminade et al., 2001a). In two conditions, the trajectory corresponded to real computerized human-hand trajectories depicting either the cursive handwriting of the first *l* of the pairs “*ll*” and “*ln*,” or the first part of a two-phase movement pointing to a “large” and a “small” target. The cinematic characteristics of the second part (i.e., the second letter of the couple, or the second phase of the pointing movement) influence the characteristics of the first, and psychophysics studies demonstrated that the perception of the first part of the movement was sufficient for subjects to decide, in a forced-choice paradigm, the expected outcome of the action.

In the neuroimaging experiment, subjects were also presented with a forced choice for the expected outcome of the actions, and the results showed that although unaware of it, they did correctly anticipate the second part of the action. Two control conditions were also used. The first one controlled for the effect of anticipation in situations free of biological motion by depicting a ball bouncing on a spring with either high or low energy, and asking the subjects whether the ball would go “near” or “far.” The second condition controlled for the visual input and motor output by depicting a ball going either to the top or the bottom of the screen, and asking the subjects to answer “top” or “down.” When we subtracted these two controls from the two conditions of interest using a masking procedure, each condition was associated with specific areas activated in the superior parietal and premotor cortices, among other areas.

Thus, tasks involving anticipation from human motion involved frontoparietal circuits that are known to be fundamental elements in the control of action (Binkofski et al., 1999a). Moreover, writing anticipation resulted in activated clusters in the left frontal operculum, which is associated with language production, and in the left superior parietal lobule, which is associated with handwriting. Anticipation of pointing yielded activated foci in the left premotor cortex and in the right intraparietal sulcus, which are associated with performance of pointing. At a covert level (since the subjects were unaware of their performances), anticipating the motor event that will follow by observing someone else activates the brain areas that are involved when actually preparing and performing the same action. This experiment provides neurophysiological support for the psychophysical model, which suggests that visual perception of human motion is partly dependent on the motor capacities of the observer. Our results therefore

strongly support the hypothesis that the neural motor system involved in the preparation and execution of action is also part of a simulation network that is used to interpret the perceived actions of others (Decety & Grèzes, 1999; Jeannerod, 1999).

Intersubjective behavior is rarely devoid of emotions and feelings. Empathy may be viewed as an other-oriented moral sentiment that fosters altruism (Sober & Wilson, 1998). This may be because an overt motivation for prosocial behavior is triggered when the self covertly (and automatically) resonates with the other (Decety, 2002b). We suggest that the perception of someone else’s emotional state also relies on shared representations, since bodily expressions are an objective, measurable output of people’s emotions.³ This view was originally proposed by Adolphs et al. to account for impaired judgment of facial expressions in patients with lesions of the primary and secondary somatosensory cortices, insula, and anterior supramarginal gyrus in the right hemisphere. These authors conjectured that the reconstruction of knowledge about other people’s emotional states might rely on a simulation of how the emotion would feel in the perceiver (Adolphs et al., 2000).

There is physiological evidence for this mechanism in the recognition of emotion from facial expression. For instance, viewing facial expressions triggers expressions on one’s own face, measured with facial electromyography, even in the absence of conscious recognition of the stimulus (Dimberg et al., 2000). There is also a single-neuron recording experiment with neurological patients that has shown that the same neurons in the anterior cingulate cortex become active both when the patients feel pain and when they watch the noxious stimulus being applied to another individual (Hutchison et al., 1999).

Decety and Chaminade (2003) designed an experiment to test the hypothesis that sympathetic feelings occur when two individuals share similar feelings and concerns and, in the context of this study, when an observer (the experimental subject) resonates with a target person (the stimulus). Note that this hypothesis reflects the way, at a commonsense level, we can automatically interrelate with other people in everyday life; it is close to what Hodges and Wegner (1997) defined as automatic empathy, as opposed to controlled empathy, and what Nichols (2001) characterized as a “concern mechanism,” which is considered to depend on a minimal capacity for mind reading and also on the affective system.

3. For relevant discussion see vol. 2, ch. 13, p. 274ff by Jesse Prinz and the comments by Huesmann, vol. 2, ch. 19.6, p. 386. ED.

Knowing that the emotions of empathy and sympathy most commonly arise when people directly perceive individuals in trouble or have a personal connection with them, we presented the subjects with dynamic stimuli that were created to elicit such feelings. For that purpose we asked semiprofessional actors to tell short stories whose narrative contents were either sad or neutral, as if they had personally experienced them. It was predicted that both the neural circuit for affective processing (namely, the amygdala and the adjacent cortices, the orbitofrontal cortex, and the insula) and the neural circuit underlying shared representations for observed and executed actions (parietal and premotor cortices) would be involved when the subject felt sympathy for the target person.

We further hypothesized that the feeling of sympathy would be disrupted or at least reduced if there was a mismatch between the narrative content of the stories and the emotional expression displayed by the actors (e.g., when a sad story was told with a happy expression). This situation may be considered, from the perspective of the viewers, as a sort of unexpected social situation, an inappropriate behavior that is less likely to produce shared feelings. We therefore predicted that neural responses in regions known to be involved in dealing with social conflict and negative affect, and accordingly, activity in the ventromedial prefrontal cortex and the superior frontal gyrus (Damasio, 1994; LeDoux, 1996), would be enhanced during the mismatch condition. In order to meet these experimental conditions, we asked the actors to tell the stories with either neutral, happy, or sad motor expressions of emotion. Their performances were videotaped and then edited to meet the constraints of a PET-activation experiment. The subjects were scanned while viewing these stimuli, and after each session they were asked to evaluate the mood of the person they had seen and how likable (in a broad sense corresponding to a feeling of sympathy) they found that person.

As predicted, in addition to a neurodynamic increase in the amygdala and adjacent cortices, cortical regions involved in the network for shared representations (namely, the dorsal premotor cortex, the pre-SMA, the central sulcus, and the inferior parietal lobule) were involved when the subjects felt sympathy with the persons who were telling sad stories. This was the experimental condition that was hypothesized to afford most concern toward others. Since the subjects performed no action during the conditions but merely watched video clips, we suggest that this network is recruited to simulate, at a covert level, the affective experiences of others (the storytellers). It is interesting to recall that according to several theorists, empathizing not only necessitates a sharing of affect, but a minimal

distinction between the self and the other is also mandatory (Reik, 1948; C. Rogers, 1959; Kohut, 1971; Povinelli & Giambrone, 1999; Decety, 2002b). The results of the present study therefore lead us to speculate that when the subjects covertly simulated the narrative content of a sad story with the intention of rating their own affinity for the communicator (i.e., how likable they found the storyteller), the distinction between their induced emotional states and the affective experiences evoked by the narrative content of the story may depend on activity in the right inferior parietal lobule. Finally, the condition of a mismatch between a sad story and a happy expression of emotion by the communicators resulted in the lowest scores in the subjects' ratings of their feeling of sympathy and, as predicted, in increased activity in the ventromedial prefrontal cortex and superior frontal gyrus. The former is associated more with dealing with social conflicts (Damasio, 1994) and the latter with sensorimotor conflicts (Fink et al., 1999).

4.5 Reciprocal Imitation, Intersubjectivity, and Agency

Mutual imitation is acknowledged to play a central role in an infant's development of intersubjectivity and shared motivational states (Nadel & Baudonnière, 1982; Nadel et al., 1999; Hobson, 1989). Role-taking during early social interactions between infant and mother are frequent and considered a milestone in the linkage between their subjective experiences. Moreover, there is good evidence that reciprocal imitation plays a constitutive role in the early development of an implicit sense of the self as a social agent (Rochat, 1999).

In order to approach these issues at a neurophysiological level, two neuroimaging experiments were designed that involved reciprocal imitation. Each experiment compared subjects imitating with subjects being imitated; that is, the subjects were either presented with new actions they had to reproduce or were asked freely to perform actions that were reproduced online by another person. The two reciprocal imitation experiments differed in the type of action and the visual feedback given to the subjects. The assumption underlying these studies was that if we compare the reciprocal imitation conditions, that is, the self imitating the other versus being imitated by the other, the sense of the moving effectors belonging to the self (i.e., what Gallagher, 2000 called the "sense of ownership"), plus the visual and somatosensory inputs, are similar or coincide. What does differ between imitating and being imitated is the relationship between the effectors and input components, which can represent oneself either as the agent

being imitated or as the imitator of the other's action. Note that in the two experiments, the behavior can be described as true imitation because the actions performed are new to the subjects in every trial, so that they are compelled to map their own actions onto the actions of the other.

The first reciprocal imitation experiment focused on mutual imitation of right-hand manipulations of an object in order to build simple constructions (Decety et al., 2002). In three conditions, the subjects manipulated the objects while watching an experimenter manipulating the same objects. The two main experimental conditions corresponded to the two situations of reciprocal imitation, in which the subjects either saw their self-triggered actions reproduced by the experimenter or had to imitate the experimenter's actions. Two other conditions in which the subjects and experimenter performed different actions and the subjects just observed the experimenter's actions were used as controls. Several key regions were involved in the two conditions of interest compared with the two control conditions; namely, the superior temporal sulcus, the inferior parietal lobule, and the medial prefrontal cortex. In the frontal lobe, activation was located in the medial prefrontal cortex, which is known to be engaged in mentalizing functions (Blakemore & Decety, 2001). Since confusion between the self and the other might occur in the two conditions of reciprocal imitation, it is interesting to find an activated cluster in this medial prefrontal region when the two conditions of imitation are compared with different actions in which such self-other confusion is not possible. When the two conditions are contrasted with each other, this region is involved, together with the pre-SMA, in the condition in which the subjects selected their own actions and saw these imitated by the other. The pre-SMA plays a functional role in temporal organization in internally guided movements (Tanji, 1994).

Another expected key region in this experiment was the inferior parietal lobule. When the two conditions of imitation were contrasted with the control condition in which the subjects acted differently from the experimenter, a lateralization of the activity in this region was found. The left inferior parietal lobule was activated when the subjects imitated the other, while the right homologous region was associated with being imitated by the other. Activation was also detected in the posterior part of the superior temporal gyrus, which is known to be involved in the visual perception of socially relevant body movements (Allison et al., 2000). This cluster was found in both hemispheres in both the conditions of imitating and being imitated, in contrast to the control condition. However, it was only present in the left hemisphere when the condition of being imitated was subtracted

from the condition of imitating the other. This lateralization in the STG is an intriguing finding, and may participate in the neural basis involved in the distinction between first- and third-person information conveyed through the visual modality. We suggest that the right STG is involved in genuine visual analysis of the other's actions, while the left region is concerned with analysis of the other's actions in relation to the intention of the self. This part of the temporal cortex is an important component in a circuit involved in social cognition (which through direct and indirect connections receives input from the ventral and the dorsal visual streams, the amygdala, the orbitofrontal cortex, and the prefrontal cortices).

Since this latter temporal region is known to be associated with biologically relevant visual inputs, one could argue that our interpretation of these results in terms of the sense of agency should be limited to the specific case of imitation of manual manipulations of objects, and should not be extended to other situations in which the self is either in control of its actions or controlled by the other. To further examine the significance of the results of this first study while excluding visual reference to body parts, we performed a second neuroimaging experiment in which the subjects were shown a white screen on which two circles of different colors were moving smoothly (Chaminade & Decety, 2002). The subjects controlled one of these circles via a computer mouse and were told that another person was controlling the other circle. In the two conditions of reciprocal imitation, the subjects were moving their circles with the intention of either leading or following the other. In the first control condition, both subjects and the other acted freely with no imitation, and in a second control condition, the subjects merely observed the other's actions.

As expected on the basis of the results of the previous experiment, activity in the medial frontal and bilateral inferior parietal cortices was detected in the contrasts between the two reciprocal imitation conditions and the control conditions. In addition, no activity in the temporal lobe was found to be associated with the two reciprocal imitation conditions. Areas related to visual processing were activated for these two conditions within the right intraparietal sulcus, and bilaterally in the lateral occipital cortex when the subjects followed the circle controlled by the experimenter. These results demonstrate that the visual association areas that are recruited shift, in the absence of sight of the body, from body-recognition areas in the temporal lobe (Allison et al., 2000) to object-oriented areas in the lateral occipital cortex (Grill-Spector, 2001).

Another fulfilled prediction was that the lateralization of the inferior parietal cortex reflected the role played by the subjects in the imitative

behavior. Left hemispheric activity was detected when they followed the experimenter, and right hemispheric activity when they saw the experimenter following their movements. The involvement of the inferior parietal cortex can no longer be explained by a visual reference to the body, and this supports our interpretation of a relation between the lateralization of activity in the inferior parietal lobule and the sense of agency (see figure 4.1).

This involvement of the inferior parietal cortex in the sense of agency is well supported by an impressive mass of converging evidence from neuropsychology (Kinsbourne, 2002) and other neuroimaging studies (Ruby & Decety, 2001; Farrer & Frith, 2002; Farrer et al., 2003), as well as from the abnormalities in attribution of intention found in schizophrenic patients experiencing passivity phenomena (S. Spence et al., 1997).

4.6 What Is So Special about the Human Inferior Parietal Cortex?

Imitation is a phylogenetically rare cognitive skill and is involved in cultural evolution. This may be the case because it is based on a rare cognitive computational ability, i.e., the intentional stance, and not just the widely present capacity for associating sensory inputs with one another and with motor outputs (Plotkin, 2002). In this chapter we have attempted to review recent functional neuroimaging studies that investigated the brain mechanisms involved in understanding actions performed by others, imitation, and in sharing mental states such as intentions and emotions. Although particular mental states can be regarded as private to their possessors, nevertheless, different individuals can share mental states of a given type by identifying with one another mentally. The similarity of activated areas (in the premotor and posterior parietal cortices) during observation of action, mental simulation, and imitation argues for a shared neural representation mechanism. However, the computational mechanisms involved in intersubjectivity cannot be reduced to this common mapping, either at the neurophysiological level or at the cognitive level. In humans, this system is interwoven with self-consciousness, as well as with the phenomenological experience of agency. Thus one highly relevant issue concerns how the self versus other distinction operates within these shared representations and which neural mechanisms are engaged in integrating and discriminating the representations activated from within and those activated by external agents.

Our functional neuroimaging studies on subjective perspective-taking, imitation, empathy, and agency, which were designed to explore both what is common to the intentional states of self and other and how they

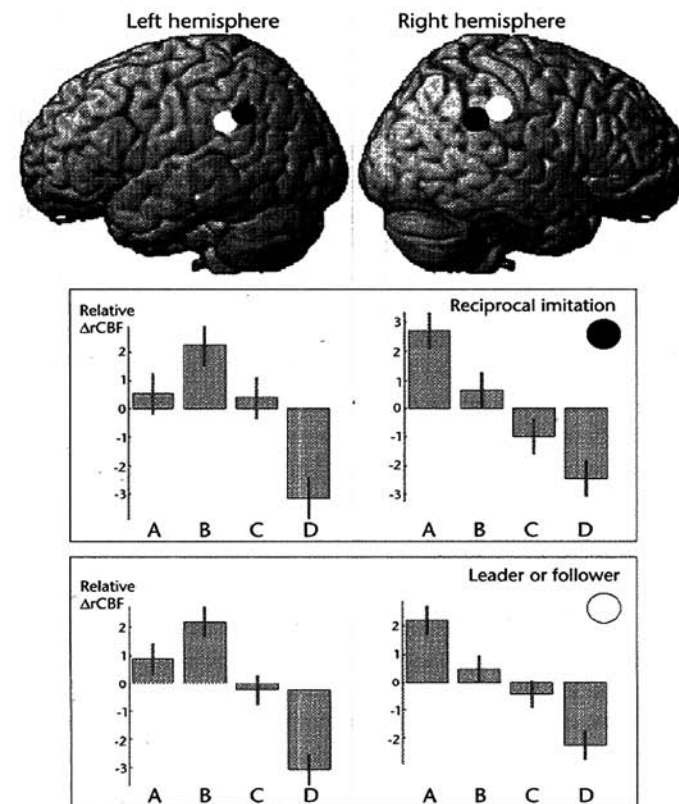


Figure 4.1

Hemodynamic activity in the inferior parietal lobule in an area in the vicinity of the posterior superior temporal sulcus during reciprocal imitation and leader versus follower experiments. The top histograms represent the relative signal change across the experimental conditions for the reciprocal imitation study by Decety et al. (2002). These are A, to be imitated; B, to imitate; C, different actions; and D, own actions. The bottom set is for the study by Chaminade et al. (2002). They are A, leading the other; B, following the other; C, acting differently; and D, observing the other's actions. Note the clear left versus right asymmetry. The right hemisphere is activated when subjects see the other imitating their actions, whereas the left hemisphere is activated when subjects imitate the actions performed by the other.

differ, have highlighted the central role of the inferior parietal cortex in intersubjective behavior, in conjunction with premotor and medial prefrontal areas in the right hemisphere. Our results also strongly suggest that the hemispheric laterality of hemodynamic activity is important and should be taken into account along with current clinical neurophysiological knowledge about the complex functions attributed to the parietal cortex in apraxia, body awareness, and more generally in higher-order representation of the body.

Other regions involved in imitation include the temporoparietal junction and the medial prefrontal cortex. The former region is activated by tasks that require processing the intention of a biological agent and are not confined to biological motion (Grèzes et al., 2001). It is also activated by speech and human sound movements (Griffiths et al., 1998). The latter region is also consistently activated in mentalizing tasks, that is, in attributing intentional states to oneself and to others (Blakemore & Decety, 2001; U. Frith, 2001), as well as in executive functioning, that is, in experiencing a cluster of high-order capacities, which includes selective attention, behavioral planning, and response inhibition (Siegal & Varley, 2002).

It is interesting that the prefrontal, inferior parietal, and temporoparietal areas have evolved tremendously in humans compared with nonhuman primates (see Passingham, 1998). The parietal cortex is roughly "after" vision and "before" motor control in the cortical information-processing hierarchy (Milner, 1998). The inferior parietal lobule is a heteromodal association cortex that receives input from the lateral and posterior thalamus, as well as visual, auditory, somesthetic, and limbic input. It also has reciprocal connections to the prefrontal and temporal lobes (D. Eidelberg & Galaburda, 1984). Note that these anatomical studies were performed in rhesus monkeys, and we don't know much about the parietal connectivity in the human brain. It remains unclear whether the monkey's posterior parietal cortex performs functions similar to those in humans, especially those related to self-awareness. It is even claimed by some scholars (e.g., Milner, 1997), following Brodmann, that the human superior parietal lobe may be equivalent to the whole of the monkey posterior parietal lobe. If so, they are at least not fully equivalent. However, it should be mentioned that mirror neurons have also been discovered in the monkey parietal area (PF; see Gallese et al., 2002).

In our studies there was more activity in the left inferior parietal lobule when subjects imitated the other, and more activity in the right homologue region when they saw their actions being imitated by the other. We postulate that the left inferior parietal lobule computes the sensorimotor

associations necessary to imitate an action demonstrated by the other, which is compatible with the literature on apraxia (e.g., Halsband, 1998), whereas the right inferior parietal lobule is involved in recognizing or detecting that the action performed by the other is similar to that initiated by the self.

There is plenty of evidence from clinical neuropsychology that the right inferior parietal cortex is important for body knowledge and self-awareness, and that lesions in this area can produce a variety of disorders related to body representation, such as anosognosia, asomatognosia, or somatoparaphrenia (Berlucchi & Aglioti, 1997). Of special interest are reports by Ramachandran and Rogers-Ramachandran (1996) of patients with right parietal lesions in whom the denial of hemiplegia can extend to the motor deficits of other patients, suggesting that the availability of an efficient body schema is necessary, not only for recognizing one's own actions, but also for understanding the actions of other individuals. It has been proposed by Heilman et al. (1998) that representation of the body must be continuously modified, updated by expectations (feedforward) and knowledge of results (feedback). Another similar formulation is that the central nervous system contains internal models that represent the current and predicted state of the motor system (Greenwald, 1970; Kawato, 1999; Berthoz, 2000). We speculate that the parietal cortex plays a major role in this mechanism through its connections with the cerebellum.

We would like to add to these accounts by proposing, in light of our neuroimaging experiments, and especially with reference to the conditions in which a subject sees his own action imitated by another individual, that the right inferior parietal lobule plays a key function (in conjunction with the right prefrontal cortex) in the unique human capacity to identify with others and thus to share subjectivities (Hobson, 1989; Meltzoff & Moore, 1998; Povinelli & Prince, 1998; Tomasello, 1999). This may well be a qualitative difference between human and nonhuman primates and not just a quantitative one. We parallel here the view developed by Povinelli and collaborators (2000) according to which the emergence of an integrated self-other representational system has occurred relatively recently (during the course of the last two million years of human evolution), and that the intimate psychological relation between the self and the other is one of the key psychological distinctions between human beings and their closest living relatives.

Finally, it is interesting to note that our abilities to represent our own thoughts and to represent another's thoughts are intimately tied together and may have similar origins within the brain (Happé et al., 1999; Keenan

et al., 2000). Thus it makes sense that self-awareness, empathy, identification, and more generally intersubjective processes are largely dependent on right hemisphere resources (Decety & Sommerville, 2003).⁴

Acknowledgment

We thank Susan Hurley for her helpful comments.

4. See the comments on this chapter by Rawlins in vol. 1, ch. 8.1, p. 195 and by Kinsbourne in ch. 8.5, p. 210. ED.