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When the self represents the other: A new cognitive neuroscience view on psychological identification

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Abstract

There is converging evidence from developmental and cognitive psychology, as well as from neuroscience, to suggest that the self is both special and social, and that self—other interaction is the driving force behind self-development. We review experimental findings which demonstrate that human infants are motivated for social interactions and suggest that the development of an awareness of other minds is rooted in the implicit notion that others are like the self. We then marshal evidence from functional neuroimaging explorations of the neurophysiological substrate of shared representations between the self and others, using various ecological paradigms such as mentally representing one's own actions versus others' actions, watching the actions executed by others, imitating the others' actions versus being imitated by others. We suggest that within this shared neural network the inferior parietal cortex and the prefrontal cortex in the right hemisphere play a special role in the essential ability to distinguish the self from others, and in the way the self represents the other. Interestingly, the right hemisphere develops its functions earlier than the left. © 2003 Elsevier Inc. All rights reserved.

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1. Introduction

Having a distinct sense of self at the phenomenological level does not mean that there is such a thing as a self, or a specific brain region dedicated to it. However, many aspects of human

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behavior seem inexplicable without the notion that each person has a self. We are aware that such a concept has many definitions and that there is no consensual framework for conceptualizing the various aspects of the self (for an exploration of various dimensions of the self from a diverse set of disciplines, see Gallagher, 2000). This complexity exists because self-processes operate at multiple levels, and different research camps have emerged to address the role of the self at these levels, but without attempting to integrate them (Robins, Norem, & Cheek, 1999). Instead of opposing a naturalistic perspective of the self to a social construction, we shall suggest that the sense of self emerges from the activity of the brain in interaction with other selves. Our formulation will be grounded in empirical evidence ranging from developmental psychology to cognitive neuroscience and clinical neuropsychology. We will suggest that self—other connectedness is underpinned by a shared representations network, which enables the self to represent the other, project thoughts and feelings to the other, feel sympathy for the other, and may also account for psychological identification with others. We will propose that the inferior parietal cortex, in conjunction with the prefrontal cortex, plays a crucial function in both self-awareness and in relating the self to others.

There is a long-standing philosophical position arguing that self and other are interconnected. For instance, in his *Treatise of Human Nature* David Hume (1739), observed that our minds are mirrors to one another: They reflect one another's passions, sentiments, and opinions. This "sympathy" or "propensity we have to sympathize with others, to receive by communication [the] inclinations and sentiments [of others], however different from, or even contrary to our own," he held to be the chief source of moral distinctions.

Contemporary research in developmental science, cognitive psychology, and neuroscience provides cumulative evidence for a view of similarities in the construction of representations of the self and others.

2. Development of self and other representations

Recent empirical studies in developmental psychology suggest that there exists an innate system that accounts for early intersubjective transactions between the self and the other. Current empirical evidence radically challenges the traditional views that considered infants as social isolates, devoid of any intersubjective link between self and other, or as being in a "normal autism" state until the age of 18 months because they confuse the self and the other (e.g., Freud, 1911).

For instance, an elegant study conducted by Rochat and Hespos (1997) demonstrated that neonates discriminate between external and self-stimulation. In this study the authors observed newborn infants when they spontaneously brought one hand to their face, touching one of their cheeks (self-stimulation), or when the experimenter's index finger touched one of the infant's cheeks (external stimulation). Microanalysis revealed that infants responded differently to the two types of stimulation. Newborns tended to display significantly more rooting responses (i.e., head turn towards the stimulation with mouth open and tonguing) following external compared to self-stimulation. Following Neisser's (1991) claim that the interpersonal self grows out of the infant's interactions with others, Rochat and Striano (2000) proposed that this interpersonal self develops via the active process of intermodal perception and exploration, in particular sensory–motor activity.

According to Tomasello (1999), humans have evolved a very special form of social cognition, namely the ability of individual organisms to understand conspecifics as beings like themselves who have intentional and mental lives like their own. This understanding enables individuals to imagine themselves "in the mental shoes" of another person, so that they can learn not just from the other, but also through the other. This could be one major difference between human and other primates. Moreover, human beings "identify" with conspecifics more deeply than do other primates. By identification, we mean the process by which an individual understands that other people are beings like herself in a way that inanimate objects are not. Interestingly, almost all analyses of identification incorporate an explicit notion of psychological inclusiveness, a consideration of how a person thinks and feels the self to be part of a larger grouping. Identification is distinct from a simple physical grouping. Through this process, each individual forms a psychological bond with others that can exist independently of any physical contact (Deaux, 1996).

Research indicates that we are from birth not only acting and thinking selves, but we also express an intuitive need to relate ourselves to other people. It has been shown that very young infants express what Trevarthen (1979) terms intersubjective sympathy, i.e., they are predisposed to be sensitive and responsive to the subjective states of other people. This can be demonstrated through several means, including spontaneous face-to-face interaction between infants and their mothers, and through more specialized "still-face procedures" (i.e., when mothers adopt a neutral face and stop responding to the infant), which can lead to withdrawal by the infant.

This relatedness with others also manifests in neonatal imitation. Studies conducted by Meltzoff and Moore (1995) have shown that imitation occurs in infants. Their experiments demonstrate that newborn infants less than one hour old can imitate facial gestures such as lip protrusion, mouth opening, and tongue protrusion. Moreover, imitation is still observed after introducing a delay between the stimulus presentation (by means of a pacifier placed in the infant's mouth) and her response. This rules out reflexes and releasing mechanisms to account for imitation. Meltzoff and Moore (1995) suggested that this innate capacity for imitation coupled with an implicit "like me" analogy provides the initial condition needed for developing more sophisticated social understanding including empathy, perspective-taking, and more advanced forms of theory of mind.

These findings have led Gallagher and Meltzoff (1996) to propose that the understanding of the other person is primarily a form of embodied practice. We develop and maintain our self-concept through the process of taking action and then reflecting on what we have done, that is, the sensory consequences of our actions, and, later in life, what others tell us about what we have done. Thus, self-concept is not innate, but is developed by the individual through interaction with the environment, as well as reflection upon that interaction. On the other hand, what might be innate and specifically human, following Tomasello's (1999) theory introduced previously and Meltzoff and Moore's (1995) "like me" analogy, and might underpin the building of the self-concept in relation with others, is the ability to identify with others, to experience that others are "like me."

A great deal of evidence has accumulated in developmental psychology showing that very young infants can and do distinguish between nonhumans and humans, and preferentially attribute mental states to the latter (Johnson, 2000). For instance, Woodward, Sommerville, and Guajardo (2001) used a visual-habituation paradigm to show infants simple object-directed actions. After infants had habituated to an actor reaching for one toy, they saw test events in which there was a change in either, the relation between the actor and her goal or the path of reach. Sixmonth-olds showed a stronger novelty response to test events featuring a change in the actor's

goal. These findings suggest that by this age infants selectively attend to the goals of actions. Furthermore, infants' propensity to attend to goals seems to be specific to human actors. Indeed, infants did not attend to the relation between actor and object for events involving inanimate actors, such as a claw.

Another compelling demonstration of infants' special self-other connectedness is illustrated by studies that show that infants imitate actions of people but not of objects (Legerstee, 1991). This result has been further explored with the re-enactment procedure used by Meltzoff (1995). This procedure capitalizes on toddlers' natural tendency to pick up behavior from adults, to re-enact or imitate what they see. Two groups of 18-month-old children were shown either a human demonstrator or a mechanical device attempting to pull apart a dumbbell. However, the human actor never produced the target action. Rather, he failed to pull the ends of the dumbbell outward, as one of his hands slipped off the object. Like the human actor, the mechanical device failed to pull apart the dumbbell, and the pincers slid off the object. Results showed that, although the children were visually riveted by both displays, the two groups of toddlers significantly differed in their tendency to reproduce the target act. Specifically children reproduced the target action after watching the human demonstrator, but they did not do so after watching the mechanical demonstration. Children apparently represent the behavior of others in a psychological framework involving goals and intended acts, instead of purely physical movements or motions.

Lastly, it was demonstrated that infants imitate things they understand. For example 15-month-olds are happy to imitate an adult putting a bird to bed, but they are less willing to put a car to bed, even after seeing an adult do so (Mandler & McDonough, 2000). Therefore, 15-month-old infants not only represent actions as goal-directed, but seem to be able to have beliefs about the goal of human actions.

Altogether, these studies establish that human infants are motivated for social interaction, and suggest that the development of an awareness of other minds is rooted in the implicit notion that others are like the self. These shared experiences are primarily based on perception and action cycles, which embody the fundamental logic of the nervous system. Indeed, the vertebrate brain was designed primitively for governing motor activity with the basic function of transforming sensory patterns into patterns of motor coordination. Herein, as expressed by Sperry (1952), lies a fundamental basis for the interpretation, direct or indirect, of all higher brain processes including mental functions. Thus, in relation to perception the motor system plays an elementary role in social cognition, and intersubjectivity develops out of overt action (i.e., transactions between self and other).

We will argue, in the rest of paper, that the right hemisphere (especially the inferior parietal cortex) plays an essential role in self-other connectedness. Interestingly, measurements of cerebral metabolism in children (aged between 18 days and 12 years) indicate a right hemispheric predominance, mainly due to the neural activity in the posterior associative areas, and that its functions develop earlier than the left hemisphere (Chiron et al., 1997).

3. Shared neural representations between self and other

The old ideomotor theory (Greenwald, 1970; James, 1890), which states that the perceptual image or idea of an action initiates performance of the action (or "thinking is for doing"), has

received considerable support from various sources, including social facilitation (e.g., Dijksterhuis & Bargh, 2001), speech perception (Liberman & Mattingley, 1985), motor mimicry (e.g., Chartrand & Bargh, 1999), motor priming (Brass, Bekkering, Wohlschläger, & Prinz, 2000), and emotional contagion (Sullins, 1991). Another more recent formulation, called the common-coding hypothesis (Hommel, Musseler, Aschersleben, & Prinz, 2001; Knoblich & Flach, 2001; Prinz, 1997), states that actions are coded in terms of the perceivable effects they should generate, and assumes that the representations of intended action effects determine action production and perception. Thus, perceiving events produced by other individuals activates the same representational structures that govern one's own planning and control of these actions (Knoblich & Jordan, 2002).

Recently the notion of shared representation 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; Grèzes & Decety, 2001). Theoretically, we propose that the meaning of a given object, action, or social situation may be, to some extent, shared by several individuals and thus should activate the same neural network in their respective brains.

Some theorists have argued that an important requirement for a full understanding of others' action is the ability to imagine performing those actions (Barresi & Moore, 1996). The involvement of common cognitive and neural resources in motor imagery (i.e., mental simulation of an action while the output is blocked) and motor behavior has received considerable support since the paper by Decety and Ingvar (1990). Numerous psychophysics experiments have shown that temporal and cinematic properties of mentally represented actions mimic those of the real represented events (for a review see Viviani, 2002).

Functional imaging exploration in subjects requested to imagine grasping objects relative to the visual inspection of the same objects results in the activation of the prefrontal cortex, the anterior cingulate, the premotor cortex, the inferior parietal lobule, the cerebellum, the ventrolateral thalamus, and the caudate nucleus in the left hemisphere (Decety et al., 1994). Lang et al. (1994) reported bilateral activations in the SMA, the precentral gyrus, and the anterior cingulate gyrus during the simulation of saccadic eye movements. Another study using internally guided motor imagery of joystick movements reported activations in the medial and lateral premotor areas, including the SMA as well as the superior and inferior parietal areas bilaterally (Stephan et al., 1995). A functional magnetic resonance imaging (fMRI) study found a significant involvement of contralateral motor cortex (30% of the activity found during actual execution) during a sequential finger-thumb opposition task (Roth et al., 1996). When asked left/right orientation judgments on images of a hand presented in their visual hemi-field, subjects cortical response is limb specific (i.e., activation in the side contralateral to the presentation, Parsons & Fox, 1998). A new study demonstrated that imagining movements of the wrist influences the kinesthetic sensation of illusory wrist movements in the absence of overt movements (Naito et al., 2002), with corresponding activation in motor cortical areas. This latter result offers a clear demonstration that imagining an action involves a sensory simulation process, which is internally generated because it was elicited neither by actual movements nor by peripheral input.

Confirmatory evidence for similarities between neural processes involved in action production and mental simulation comes from studies of neurological patients, which demonstrate that motor-performance deficits are reflected in motor imagery. For instance, Dominey, Decety,

Broussolle, Chazot, and Jeannerod (1995) examined hemi-Parkinson patients in both visual and motor imagery tasks involving either side of the body. They reported a selective deficit in motor imagery, but not in visual imagery, on the affected side that closely matched the deficit in actual motor performance. Patients with lesions restricted to the parietal cortex were found to be selectively impaired at predicting, through mental imagery tasks, the time necessary to perform finger movements, in comparison to normal subjects (Sirigu et al., 1996). A similar observation has been reported in a single case study of a patient with severe ideomotor apraxia who was selectively impaired in motor imagery while his capacity in visual imagery of objects was spared (Ochipa et al., 1997).

Unlike the studies on mental simulation that can be carried out solely with humans, the exploration of the neural correlates of the perception of others' actions is carried out in both human and nonhuman primates. An impressive array of data supports the idea of a common mental code for perceived actions and action performed by the individual himself.

Electrophysiological recordings in the rostral part of the monkey inferior premotor cortex (area F5) have indicated that there are neurons that discharge during execution of hand and mouth movements. Some years later, the same authors discovered that most of these neurons discharge not only when the monkeys performed an action, but also when the monkey observed the experimenter making a similar action (e.g., Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). Neurons that exhibited such properties were therefore called "mirror neurons." A subset of these mirror neurons also respond when the final part of an action, crucial in triggering the response in full vision, is hidden, and can therefore only be inferred (Umilta et al., 2001). This finding is compatible with the idea that we understand actions when we map the visual representation of the observed action onto our motor representations of the same action (for a recent review see Rizzolatti, Fogassi, & Gallese, 2001). Neurons sensitive to the sight of complex body movements and particularly to the detection of where another animal is directing its attention have also been discovered in the monkey anterior superior temporal sulcus (see Jellema & Perrett, 2002). However, these neurons do not express motor-related activity, and this region is not directly connected to the ventral premotor cortex. Interestingly, both area F5 and STS are linked to area PF located in the anterior part of the inferior parietal cortex, where a cluster of neurons were recently found to exhibit mirror properties, i.e., motor properties that match the visual ones (Gallese, Fadiga, Fogassi, & Rizzolatti, 2002).

Evidence for a mirror system in human comes from various studies using different neuroimaging techniques. Fadiga, Fogassi, Pavesi, and Rizzolatti (1995) demonstrated with magnetic transcranial stimulation (TMS) an increase in excitability of the motor system during the perception of actions performed by another individual. This enhancement of motor system is selective since it occurred in the muscles that the subjects would use for producing the action observed. Converging evidence was reported in a study that used EEG cartography during the perception of different sorts of video movies consisting of objects in movement, animals in motion, gymnastic movements executed by a person, and still shots (Cochin, Barthelemy, Roux, & Martineau, 1999). Significant decreases in the $\alpha 1$, $\beta 1$, and $\beta 2$ power values of the EEG over the centro-parietal regions, in both hemispheres, were shown during the perception of human motion sequences. Their results suggest the specific participation of the sensorimotor cortex during the observation of human motion. Magnetoencephalographic recordings have also shown activation of the precentral gyrus during action observation (Hari et al., 1998). More recently, it has been shown that the perception of others' action activates the premotor cortex and the parietal cortex in a somatotopical manner, namely watching mouth actions activates the cortical representation of the mouth, while watching hand or foot actions activates their respective representations (Buccino et al., 2001).

4. The effect of the intention (or to be an agent)

To investigate the role of intention on the activation of the neural network that is activated during the observation of action, a series of studies performed by our group manipulated the cognitive strategy of the subjects while watching human actions. In the studies, participants were instructed to either memorize the action for later imitation or for later recognition (Decety et al., 1997; Grèzes, Costes, & Decety, 1998; Grèzes, Costes, & Decety, 1999). When subjects observed actions for later imitation as compared with passive observation of the same actions, 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 subjects were observing the actions for recognition purposes. In that case, the parahippocampal gyrus in the temporal lobe was chiefly activated. There is thus a top-down effect of intention upon the information processing involved in action observation. Observing in order to imitate tunes regions involved in action generation to a step beyond simple motor resonance, which corresponds to motor preparation and is likely to involve executive functions subserved by the prefrontal cortex. Note that in all of these studies, the right inferior parietal cortex was consistently found activated in conditions of observation for later imitation. When conditions of observation of actions were contrasted with static posture, increased activity was detected in the premotor cortex at the level of the upper limb representation, a result compatible with the mirror neuron discovery in the monkey.

Altogether, these studies strongly support the view that action observation involves neural regions similar to those engaged during actual action production, and that this network may be modulated by the intention of the observer.

Moreover, this motor resonance phenomenon seems to be selectively triggered by actions that belong to the motor repertoire of the subject watching them. Stevens, Fonlupt, Shiffrar, and Decety (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, subjects were shown either possible or impossible biomechanical paths of apparent motion. The left primary motor cortex and the parietal cortex were found to be selectively activated when subjects perceived possible paths of human movement. No selective activation of these areas was found during conditions of biomechanically impossible movement paths. Additional support for the involvement of implicit motor knowledge during observed actions derives from a PET study in which participants were presented with the first trajectory component of a dot depicting either mechanical, pointing, or writing movements, and were asked to anticipate the outcome of that dot (Chaminade, Meary, Orliaguet, & Decety, 2001). As predicted from the theory, perceptual anticipation of human actions resulted in activation of the cortical areas involved in the covert stages of the corresponding action. Selective activation of

the left premotor cortex and of the right intraparietal sulcus was associated with the perception of pointing movements, whereas the left frontal operculum and superior parietal lobule were associated with the perception of writing movements.

Taken together, the results of the above-mentioned functional neuroimaging studies strongly support the view that during the observation of actions produced by other individuals, and during the imagination of one's own actions, there is specific recruitment of the neural structures which would normally be involved in the actual generation of the same actions. These results are clearly consistent with the notion that the perception of bodily movements is mediated (and maybe even constrained) by implicit motor knowledge (Shiffrar & Pinto, 2002), and that we may understand the actions of others in terms of our own motor system (Blakemore & Decety, 2001).

The shared representations model may also be applied to the processing of emotions (Adolphs, 2002). In this model, perception of emotion would activate the neural mechanisms that are responsible for the generation of emotions. Such a mechanism would prompt the observer to resonate with the state of another individual, with the observer activating the motor representations that gave rise to the observed stimulus, i.e., a sort of inverse mapping. For example, while watching someone smile, the observer would activate the same facial muscles involved in producing a smile at a subthreshold level and this would create 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 (Dimberg, Thunberg, & Elmehed, 2000; Wallbott, 1991). Converging neurophysiological arguments in favor of this model are supported by the finding that right somatosensory-related cortices are necessary in both expressing and recognizing emotions (Adolphs, Damasio, Tranel, Cooper, & Damasio, 2000). Interestingly, a single-neuron recording study in neurological patients has shown that there are pain-related neurons in the anterior cingulate cortex (ACC) that respond both to actual stimulation (thermal stimuli) and also to the observation of the same stimuli delivered to another individual (Hutchison, Davis, Lozano, Tasker, & Dostrovsky, 1999). Altogether, shared representations at the cortical level has been found in action, pain processing, and emotion recognition, which would give us a neurophysiological basis for the operation of social cognition. A recent neuroimaging study has demonstrated the involvement of shared representations (in both emotion processing areas, and fronto-parietal networks) when subjects feel sympathy for another individual (Decety & Chaminade, 2003).

Thus, the concept of shared representations seems well supported by empirical evidence, and more generally, one may advocate that within a given cultural group, the meaning of a given object, action, or social situation may be common to several individuals and thus should activate the same mental code. This code would be mediated by a similar neural network in their respective brains. There is no reason to see shared representations tapping only pragmatic representations, because they could also address semantic and affective representations. This would also explain why we come to understand that others are like us at the psychological level, and extrapolate their mental states (intentions, desires, and beliefs). This line of reasoning parallels the simulation theory in philosophy of mind, which maintains that one represents the mental activities and processes of others by generating similar activities and processes in oneself (Gordon, 1986; Goldman, 1989).

5. Self-awareness as an essential component for navigating within the shared representations

Even if others are apparently like us, they are never exactly like us, and under normal circumstances, we do not confuse others with ourselves. The idea of a common mental code involved in self-initiated (performed or imagined) actions and in perceiving the behavior of others does not mean an overlap between the two signals. Without a sense of self-awareness (and perhaps self-consciousness), we will just resonate with one another, become distressed by the distress of others, and certainly will not be able to consciously represent the other, or feel empathy for her.

An 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 or proprioception), which are both crucial to the normal adult's understanding of social cognition and intersubjectivity, activate an internal intentional schema (Barresi & Moore, 1996). This schema would have the capacity to coordinate first-person and third-person information and compute the attribution of action to the self or to the other.

There is much evidence that the prefrontal cortex plays a key role in self-consciousness including self-ownership (i.e., it is my body that is moving), and self-agency (i.e., I am the initiator of the action, thought or desire). These high level functions tap executive functions resources, including inhibition, which are necessary for the initiation and the maintenance of nonautomatic cognitive processes (Ferstl & von Cramon, 2001, 2002). Lesions of the prefrontal cortex may cause dysfunction in self-monitoring and lead to what Lhermitte, Pillon, and Serdaru (1986) termed the "environmental dependency syndrome." We suggest that the prefrontal cortex plays a central role in coordinating self and other representations by monitoring signals from executive and sensory regions, and identifying the source of perceptions (internal or external).

Another formulation draws on the concept of internal models that rely on feedback and feed forward mechanisms (Greenwald, 1970; Wolpert & Kawato, 1998). It has been suggested that the same process used by the forward model to predict the sensory consequences of one's own movements could be used to estimates intentions from the observation of other person's actions (Blakemore & Decety, 2001). We will discuss this model further after presenting our work on reciprocal imitation.

6. Reciprocal imitation as a natural paradigm to explore self-other connectedness

One way to empirically investigate both the similarities and differences in the hemodynamic response in ecologically valid social interactions is to use mutual imitation paradigms. Mutual imitation is acknowledged to play a central role in infant development of intersubjectivity and shared motivational states (Hobson, 1989; Nadel & Baudonnière, 1982). 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 self as social agent (Rochat, 1999). One should bear in mind that imitation is a molar construct, and a careful analysis of the subcomponents implicate a whole sequence of molecular processes at work, such as

visual attention, cross-modal transfer, motor production, memory for representations, motivation or intentionality, representation of the body schema, and action monitoring (Rogers, 1999).

In reciprocal imitation situations, a similar action is executed by one individual who is watched and imitated by another individual, after which the roles are reversed. Using such situations in neuroimaging experiments allowed us to investigate the sense of being the source of our actions when both the observation and the execution neural networks are similarly activated.

In order to tackle the neural correlates of agency, two positron emission tomography experiments were performed in which the participants were either presented with new actions they had to reproduce, or freely performed actions that were reproduced on-line by another person. These studies differed as to the type of action and the visual feedback given to the subjects. The hypothesis underlying these studies was that, in the reciprocal imitation conditions, when the self is imitating the other or being imitated by the other, both the sense of the moving effectors that belong to the self [i.e., what Gallagher (2000) called the sense of ownership], as well as the visual and somatosensory inputs, would be similar and would coincide. The relationship between these two components would differ however. In one case, one can make oneself the agent of one's own action (when being imitated), or one can simply be shown how to act by the other (to imitate). Note than in the two experiments, the behavior can be described as real imitation because the actions performed are in every case new to the subjects, so that they are compelled to map their own actions onto the actions of the other.

The first experiment focused on mutual imitation of right-hand object manipulations in order to build simple constructions (Decety, Chaminade, Grèzes, & Meltzoff, 2002). In three conditions, 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 own actions reproduced by the experimenter or had to imitate the experimenter's actions. In two other control conditions, the subjects and experimenter performed different actions and the subjects just observed the experimenter's actions. Several brain regions were involved in the two conditions of imitation compared to the two control conditions, namely the superior temporal sulcus, the inferior parietal lobule, and the medial frontal cortex. When the two conditions of imitation were contrasted to the control condition in which subjects acted differently from the experimenter, a lateralization of the activity in the inferior parietal lobule was found. The left inferior parietal lobule was activated when subjects imitated the other, while the right homologous region was associated with being imitated by the other.

¹ There are many definitions of imitation. Yet, we will probably all agree that imitation is a natural mechanism that involves perception and action coupling. Where we will probably start to disagree, despite a flurry of interest in imitation, is whether it is a specific human capacity or whether nonhuman primates share this ability. Here, we take the stance along with many developmental psychologists that imitation does not only rely on the widely present capacity for associating sensory inputs with one another and with motor outputs, but that imitation is intentional and effortful. We do apply strict criteria for the definition of imitation, namely the novelty of the behavior and the similarity of the goal and of the means to achieve it. Thus, imitation is not a mindless matching behavior, but reflects rather sophisticated cognitive processing. This is different from other forms of social learning, such as emulation (reproducing the goal without necessarily replicating the specific actions of the model), or mimicry (the duplication of a behavior without understanding the goal of that behavior).

In the frontal lobe, an activated cluster was found in the medial prefrontal cortex, which is known to be involved in executive functioning (Ferstl & von Cramon, 2002). The pre-SMA was found to be activated in the condition where subjects selected their actions and saw these imitated by the other, which is coherent with its role in the temporal organization of internally guided movements (Tanji, 1994). Taken together, activations in the prefrontal cortex account for the crucial executive component of imitation (Rogers & Pennington, 1991).

Activation was also detected in the posterior part of the superior temporal gyrus (STG). This region is known to be involved in the visual perception of socially meaningful body gestures (Allison, Puce, & McCarty, 2000), and more generally in tasks that require detection of biological agents, such as perception of biological motion (Grèzes et al., 2001; Grossman & Blake, 2001), and also the perception of speech and human sound movements (Griffiths et al., 1998). 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 both the ventral and dorsal visual streams, the amygdala, the orbitofrontal cortex, and the prefrontal cortices). This cluster of activity was found in both hemispheres when contrasting the conditions of imitating and of being imitated to the condition of self-action. 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 could be involved in genuine visual analysis of the other's actions, while the left region could be concerned with the analysis of the other's actions in relation to the intention of the self.

Since this part of the temporal cortex at the junction with the parietal cortex is involved in the processing of biologically relevant sensory inputs, one could argue that our interpretation of the results in the context of the sense of agency is limited to the specific situation of imitation of hand manipulations of objects, and may not be extended to other situations in which the self is in control of its actions or controlled by the other.

To further examine the significance of the results of this first study, and to exclude visual reference to body parts, second neuroimaging experiment was conducted in which subjects were shown a white screen on which two circles of different colors were moving smoothly (Chaminade & Decety, 2002). 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, subjects were moving their circles with the task to either lead or follow the other person. In a first control condition, both subjects and the other acted freely, while in a second control condition subjects observed the actions made by the other. As expected on the basis of the results of the previous experiment, medial frontal and bilateral inferior parietal cortices were detected in the contrasts between the two reciprocal imitation conditions and the observation control. In addition, no activity in the temporal lobe was found to be associated with the two conditions of interest. Visual-processing related areas were activated for the two conditions within the right intraparietal sulcus, and bilaterally in the lateral occipital cortex when subjects followed the experimenter. These results demonstrate that, when the body is not seen, the visual association areas recruited by the task shift from body-recognition in the temporal lobe to object-oriented in the lateral occipital cortex (Grill-Spector, Kourtzi, & Kanwisher, 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 were followed by the experimenter. Therefore, the involvement of the inferior parietal lobule 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.

In the two functional imaging studies described above, there was more increase in the left inferior parietal lobule when subjects' actions were initiated by the other, and more increase in the right homologue region when they controlled the others' actions. We postulate that: (1) the left inferior parietal lobule computes the sensory-motor associations necessary to imitate an action demonstrated by the other, which is compatible with the literature on apraxia (e.g., Halsband, 1998), and (2) 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. Therefore the lateralization of the inferior parietal cortex activity in relation to the sense of agency could be defined in similar terms as those introduced by Barresi and Moore (1996) in their description of the monitoring of first- and third-person information, applied to the control of action. The left hemisphere, dominant for the execution of action, is over-activated when the intention comes from a third-person via the visual modality, while the right hemisphere is more activated when the intention of the self (first-person), is reflected in an other individual, a third person input. We thus postulate that the link between the control of action, the first-versus third-person monitoring, and the sense of agency are related phenomenon involving the inferior parietal lobule in conjunction with the prefrontal cortex.

7. The inferior parietal cortex and the sense of agency

There is plenty of evidence from clinical neuropsychology that lesions to the inferior parietal cortex in the language-dominant hemisphere are associated with apraxia and aphasia (Freund, 2001). Several authors argued that the different types of apraxia could be ascribed to lesions in the two systems of motor control, a conceptual system and a production system (e.g., Leiguarda & Marsden, 2000). The inferior parietal cortex in the dominant hemisphere is part of the conceptual system. Rothi, Ochipa, and Heilman (1991) proposed that this region would be the cortical location where "visuokinaesthetic motor engrams" are stored. This directly parallels the ideomotor theory introduced previously, and further confirms the role of the left inferior parietal cortex in associating actions and their sensory consequences. The right inferior parietal lobule subserves different functions as demonstrated by lesion studies. For instance, unilateral neglect, which has been consistently associated with lesions in the right inferior parietal cortex (Marshall, Fink, Halligan, & Vallar, 2002), is described as the inability "to perceive or conceive the existence of the left side of somatic and extrasomatic space" (Bisiach, 1999). While the left 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). Of special interest here, Ramachandran and Rogers-Ramachandran (1996) have reported the cases of patients with right parietal lesions in whom the denial of hemiplegia can extend to the motor deficits of other

patients, suggesting that 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.

The involvement of the inferior parietal cortex in the sense of agency itself is well supported by an impressive mass of converging evidence in addition to the work reported here, including neuropsychology (Kinsbourne, 2002), other neuroimaging studies in healthy subjects (e.g., Farrer & Frith, 2002; Farrer et al., 2003; Ruby & Decety, 2001, 2003), as well as a study of abnormalities in attribution of intention found in schizophrenic patients experiencing passivity phenomena, which resulted in a dramatic activation of the right inferior parietal cortex (Spence et al., 1997). Recently, 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).

Interestingly, not only the prefrontal, but also the inferior parietal and temporo-parietal areas have evolved tremendously in humans as compared to nonhuman primates (Passingham, 1998). The parietal cortex appears roughly "after" vision and "before" motor control in the cortical information-processing hierarchy (Milner, 1998). It is a heteromodal association cortex which receives input from the lateral and posterior thalamus, as well as visual, auditory, somaesthetic, and limbic areas. It has reciprocal connections to the prefrontal cortex, and to the temporal lobes (Eidelberg & Galaburda, 1984). Note that these anatomical studies were performed in rhesus monkeys, and we do not know much about its connectivity in the human brain. It remains unclear whether the monkey's posterior parietal cortex performs similar functions as in humans. And it is even claimed by some scholars (e.g., Milner, 1997), following Brodmann's work, that the human superior parietal lobe may be equivalent to the whole of the monkey posterior parietal lobe. There would thus be no monkey equivalent to the human inferior parietal lobe, or at least, not completely equivalent.

It has been proposed by Heilman, Barrett, and Adair (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 which represent the current and predicted state of the motor system (Frith, Blakemore, & Wolpert, 2000). To be computed, these internal models need to be able to represent the state of the body and to be associated, directly or via association cortices, with sensory and motor cortices. The posterior parietal is indeed connected both to the sensory and to the premotor cortices, as well as to the limbic system. In this model, the represented state of the body is updated by computation using the efference copy (a copy of the motor program) as input in a feedforward fashion, and this updated representation is compared to the real state of the body using the multisensory feedback as input. As a consequence, this representation maps the relation between the motor program and its sensory consequences. We argue that the inferior parietal lobule plays a major role in this mechanism in relation to the control of complex actions, such as hand actions and speech. Based on our results, one simple hypothesis would be that imitation involves assembling a motor program to match the observed action performed by another individual, which can also be described as choosing the correct representation or internal model based on sensory input in order to recruit the corresponding motor program. The central role of the left inferior parietal cortex in this type of task is clearly supported by neuropsychological observations, and more recently by the neuroimaging experiments described in this article.

8. Psychological identification with others

The capacity to identify with other conspecifics, considered a prerequisite to feeling sympathy and empathy (Decety, 2002; Hobson, 1989, 2002; Tomasello, 1999), is a distinctive characteristic of human beings that other primates apparently do not possess (Povinelli & Giambrone, 1999). Newborns are innately highly attuned to other people and motivated to socially interact with others. From the earliest months of their lives, 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 the movements 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 from biological (human) and nonbiological effector system (robot) have shown only the former to induce such effects (Castiello, Lusher, Mari, Edwards, & Humphreys, 2002).

In one neuroimaging study that used virtual reality, no premotor nor inferior parietal activation was detected when participants were shown a virtual hand grasping objects (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, produced by another biological agent, and, as a consequence, more difficult to identify with. In other words, their motor systems did not resonate with the observed ones, as it is the case when the hand is real. To further test the hypothesis that only the perception of naturalistic actions maps onto existing action representations, Perani et al. (2001) presented subjects with object-grasping actions performed either by a real hand or by means of 3D-virtual reality or 2D-TV screen. Results showed common activation foci in the left posterior parietal cortex and in the premotor cortex, both for observation of real-hand actions and artificial ones, with greater signal increase for the real-hand condition. A striking finding was the selective involvement of the right inferior parietal cortex and the right superior temporal gyrus only in the condition of observation of real hand actions.

In addition to these accounts, we would like to submit, in light of the neuroimaging experiments reviewed here, and especially in those conditions in which subjects watched their actions imitated by another individual, that the right inferior parietal lobule plays a key function in the capacity unique to human beings to identify with others and thus share subjectivities. In terms of neural mechanism, it could be explained by the automatic activation of the shared motor representations in the inferior parietal cortices corresponding to the observed action via the "reversed" inverse model discussed earlier (from sensory consequences to the motor program) only when the sensory inputs emanate from a human agent.

Thus it can be proposed that the human system involved in the perception and understanding of actions performed by other selves might be based, as postulated in the rest of the chapter, not only on a direct matching neural mechanism between perception and action, but that it also requires identification with the other, as well as the capacity to distinguish the self from other selves, and to be aware being the source of our actions (including thoughts and desires). We believe that such mechanisms are necessary to experience intersubjectivity. 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.

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, Bering, and Giambrone (2000) according to which the emergence of an integrated self—other representational system has occurred relatively recently (during the course of the last 2 million years of human evolution), and that the intimate psychological relation between self and other is one of the key psychological distinctions between humans and their closest living relatives.

9. Conclusion

In this article we attempted to review functional neuroimaging studies that investigate the brain mechanisms involved in understanding actions performed by others, imitation, and in sharing mental states such as intentions and emotions. Mental states that are in essence private to the self may be shared between individuals. The similarity of activated areas (in premotor and posterior parietal cortices) between observation of action, mental simulation, and imitation accounts for a shared neural representation model. However, the mechanisms involved in intersubjectivity cannot be reduced to this common mapping, neither at the neurophysiological level nor at the cognitive level. This system is interwoven with self-consciousness, as well as with the phenomenological experience of agency. Thus one highly relevant issue, both in neuropsychology but also from an evolutionary perspective, 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 by the self and those are activated by external agents. Our work suggests the inferior parietal cortex in conjunction with prefrontal areas plays an important role in how the self relates to other, as well as in the sense of agency.

Finally, it is interesting to note that our ability to represent one's own thoughts and represent another's thoughts are intimately tied together and may have similar origins within the brain (Keenan, Wheeler, Gallup, & Pascual-Leone, 2000). Thus it makes sense that self-awareness, empathy, identification with others, and more generally intersubjective processes, are largely dependent upon the right hemisphere resources, which are the first to develops.

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