

CHAPTER 4

Mirror neurons and intersubjectivity

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Introduction

By observing mother-infant interactions during early infancy, it is clear that a play of mutual exchange between mother and infant is taking place. Such mutual exchange between mother and child may take the form of timing their behaviours, such as the onset of facial expressions, or of anticipating other's intentions. This can be further noticed in the ability of the infant to detect when this correspondence is temporarily broken. A further evidence of forms of intersubjectivity taking place during infancy is early imitation (Meltzoff & Moore 1977) and cross-modal imitation, or affect attunement (Stern 1985).

In the last few decades, the evidence accumulated in developmental psychology (Trevarthen 1974, 1979, 1980; Stern 1985, 2004) favours the idea that very early during development the infant is endowed with an innate capacity of subject-subject engagements, in a game of bi-directional communication that enables him/her of direct alteroception or even as Bråten (1998) defines it, of "alter-centred participation". This new perspective in developmental psychology represents a breaking point with the Freudian and Piagetian legacy anchored to auto- and ego-centric assumptions.

These findings on infant-mother relationship clearly indicate that our nervous system has been constructed in such a way that it enables us to capture others' living experiences just by watching them. This construction is built up in order to respond and re-act at very early stages during life.

In this chapter we will address the central question of which neural mechanisms may underpin such capability. We will posit that the mirror neuron systems, together with other mirroring neural clusters outside the motor domain, constitute the neural underpinnings of embodied simulation, the functional mechanism at the basis of intersubjectivity. We will also provide behavioural evidence that such a system can be at the basis of several social-cognitive phenomena in human and

nonhuman primates. This will help in delineating a possible evolutionary scenario in which intersubjectivity emerged.

Here we employ the term “embodied simulation” as an automatic, unconscious, and pre-reflexive functional mechanism, whose function is the modelling of objects, agents, and events. Simulation, as conceived of in the present paper, is therefore not necessarily the result of a willed and conscious cognitive effort, aimed at interpreting the intentions hidden in the overt behaviour of others, but rather a basic functional mechanism of our brain and we will propose that this basic functional mechanism is sub-personally instantiated by mirror neurons. In addition, because it also generates representational content, embodied simulation seems to play a major role in our epistemic approach to the world. It represents the outcome of possible actions, emotions, or sensations one could take or experience, and serves to attribute this outcome to another organism as a real goal-state it is trying to bring about, or as a real emotion or sensation it is experiencing. By means of embodied simulation, we are *intentionally attuned* to others (see Gallese 2005).

Mirror neurons: Monkey data

About ten years ago Rizzolatti and colleagues discovered a class of premotor visuo-motor neurons, named *mirror neurons*, that discharge not only when the monkey executes goal-related hand actions like grasping objects, but also when observing other individuals (monkeys or humans) executing similar actions (di Pellegrino et al. 1992; Gallese et al. 1996; Rizzolatti et al. 1996). Neurons with similar properties were later discovered in a sector of the posterior parietal cortex reciprocally connected with area F5 (PF mirror neurons, see Rizzolatti et al. 2001; Gallese et al. 2002).

The most interesting property of mirror neurons consists in the fact that in most of them there is a good congruence between the seen and the executed actions effective in activating them. Because of this congruence, it was hypothesized that mirror neurons, by matching action observation with action execution, allow understanding of actions made by others. This latter capacity is not simply limited to recognition of motor patterns, but it extends also to the goal of the observed action. Every time we observe an action made by another individual, we are able to understand its goal because the observed action is matched on our internal representation of it, which, in turn, is endowed with the knowledge of the goal.

Further studies carried out in our lab corroborated and extended our original hypothesis. We showed that F5 mirror neurons are also activated when the final critical part of the observed action, that is, the hand-object interaction, is hidden (Umiltà et al. 2001). In a second study we showed that a particular class of F5

mirror neurons, “audio-visual mirror neurons” can be driven not only by action execution and observation, but also by the sound produced by the same action (Kohler et al. 2002). These neurons instantiate semblant informational content at quite an “abstract” level. If the various modes of presentation of events as intrinsically different as sounds, images, or voluntary body actions, nevertheless are bound together within the same neural substrate, what we have is a mechanism instantiating a form of conceptualization. This perspective can be extended to other parts of the sensory-motor system (see Gallese & Lakoff 2005).

In a recent study (Ferrari et al. 2005) it has been shown that mirror neurons can generalize the goal of an action to actions that are not in the monkey motor repertoire such as those made with a tool. What is interesting here is that what is coded, at a very abstract level, is the goal of an action even though the monkey is not able to reproduce it. The fact that the visual descriptions of actions outside the motor repertoire can map onto one’s own motor system supports the idea that the sensory description of observed social stimuli is strongly related (embodied), and somehow interpreted, to the observer’s own body sensory-motor knowledge.

So far, the capability of monkey mirror neurons to connect the observed individual with the observer seems to configure a mechanism that can be useful in understanding actions but with no necessity to directly interact with another individual. It is as if we were watching a TV movie in which we observe and interpret the events that unfold in a story. However, the mirror neuron story becomes more complex in the light of the recent findings of a new category of mirror neurons that are related to the execution/observation matching system for mouth actions (Ferrari et al. 2003). Most mouth mirror neurons, as they have been named, respond to observation of ingestive actions such as biting, tearing with the teeth, sucking, licking, etc. An example of an “ingestive” mouth mirror neuron is shown in Figure 1, A. They show the same specificity of hand mirror neurons. They do not respond to simple object presentation or to mouth mimed actions.

An interesting finding is that a small percentage of mouth-related mirror neurons discharge during the observation of intransitive, communicative facial actions performed by the experimenter in front of the monkey (“communicative mouth mirror neurons”), such as lips-smacking, lips protrusion or tongue protrusion. Figure 1, B and C shows two examples of “communicative” mouth mirror neurons. The motor response of mouth communicative mirror neurons is more complex. In those neurons in which it was possible to test the motor response during monkey execution of communicative actions, there was a clear activation (Figure 1, C). However, most neurons responded also when the monkey executed ingestive actions. It has been hypothesized that the presence of mouth mirror neurons is indicative of a system originated for understanding transitive mouth ac-

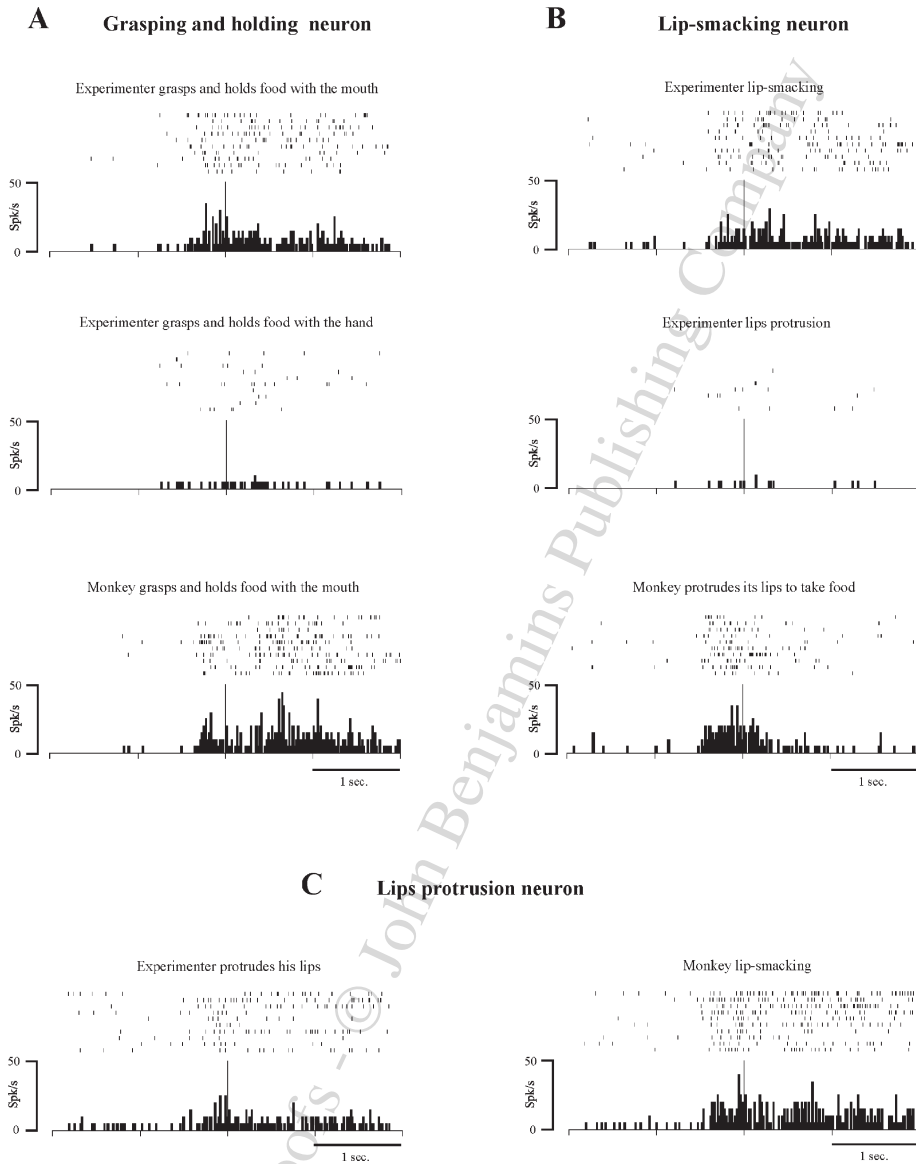


Figure 1. Examples of mouth mirror neurons. In each panel the rasters and the histograms represent the neuron response during a single experimental condition. The histogram represents the average of ten trials. Rasters and histograms are aligned with the moment in which the mouth or the hand of the experimenter (observation conditions) or of the monkey (motor conditions) touched the food or when the food is abruptly presented (presentation conditions). During observation of communicative actions the rasters and histograms alignment was made with the moment in which the action was fully expressed. Ordinates: spikes/sec; abscissae: time; bin width: 20 ms. A. Ingestive mouth mirror neuron.

tion and subsequently it has been exploited to evolve an oro-facial communicative system (Ferrari et al. 2003; Fogassi & Ferrari 2004).

The properties of mouth mirror neurons, and in particular of the “communicative” ones, could constitute an emergent property of the monkey mirror neurons in which the open access to others’ experiences by means of the observer’s own body-related knowledge is also extended to oro-facial actions which may imply a direct participation of the observer in a dyadic communication. Thus, this new property of mirror neurons would open a new possibility for the system in such a way that the flow of social information is not unidirectional (from the observed agent to the observer) but it also encompasses a bi-directional mutual exchange, a new intersubjective space or an *intersubjective matrix* as defined by Stern (2004).

The mirror neuron system for actions in humans

Several studies using different experimental methodologies and techniques have demonstrated also in the human brain the existence of a mirror neuron system matching action perception and execution. During action observation there is a strong activation of premotor and parietal areas, the likely human homologue of the monkey areas in which mirror neurons were originally described (for a review, see Rizzolatti et al. 2001; Gallese 2003a; Rizzolatti & Craighero 2004; Gallese et al. 2004). Furthermore, the mirror neuron matching system for actions in humans is somatotopically organized, with distinct cortical regions within the premotor and posterior parietal cortices being activated by the observation/execution of mouth, hand, and foot related actions (Buccino et al. 2001).

A recent brain imaging study, in which human participants observed communicative mouth actions performed by humans, monkeys and dogs showed that

Figure 1. *Top.* The experimenter approaches with his mouth the food held on a support, grasps it with the teeth and holds it. *Middle.* The experimenter grasps with the hand a piece of food placed on a support and holds it. *Bottom.* The experimenter moves a piece of food to the monkey’s mouth; the monkey grasps and holds it with its teeth. **B.** Communicative mouth mirror neuron. *Top.* The experimenter makes a lip-smacking action looking at the monkey. *Middle.* The experimenter protrudes his lips looking at the monkey. *Bottom.* The experimenter moves a piece of food toward the monkey’s mouth; the monkey protrudes its lips and takes the food. **C.** Communicative mouth mirror neuron. *Left.* The experimenter protrudes his lips looking at the monkey. *Right.* During the experimenter lips protrusion the monkey responds almost simultaneously to the experimenter gesture by making a lip-smacking action. Modified from Ferrari et al. (2003).

the observation of communicative mouth actions led to the activation of different cortical foci according to the different observed species. The observation of human silent speech activated the pars opercularis of the left inferior frontal gyrus, a sector of Broca's region. The observation of monkey lip-smacking activated a smaller part of the same region bilaterally. Finally, the observation of the barking dog, activated only extrastriate visual areas. Actions belonging to the motor repertoire of the observer (e.g., biting and speech reading) or very closely related to it (e.g. monkey's lip-smacking) are mapped on the observer's motor system. Actions that do not belong to this repertoire (e.g., barking) are mapped and henceforth categorized on the basis of their visual properties (Buccino et al. 2004).

The involvement of the motor system during observation of communicative mouth actions is also testified by the results of a TMS study by Watkins et al. (2003), in which they showed that the observation of communicative, speech-related mouth actions, facilitate the excitability of the motor system involved in the production of the same actions.

Mirror neurons and primary intersubjectivity: Behavioural studies on synchrony and infant imitation in human and nonhuman primates

When writing about neural correlates of intersubjectivity, Stern in his recent book pointed out an interesting issue: "To resonate with someone, you may have to be unconscious in synch with that person. You could move in synchrony, as lovers may do when they sit across a coffee table and trace a dance as they simultaneously approach and withdraw their faces from one another or move their hands together at the same instant" (Stern 2004: 80).

What do mirror neurons tell us about synchrony and resonance? Is it possible to formulate and test hypotheses in the examination of these phenomena? Rizzolatti et al. (1999) used a metaphor to better elucidate how we understand the actions of others through the mirror mechanism. We understand other's actions through a mechanism of *resonance*, in which the motor system of the observer "resonates" (i.e. mirror neurons activation) whenever an appropriate visual and/or acoustic input is presented, although it does not necessarily imply the production of an overt movement. Rizzolatti and coworkers (1999, 2002) proposed that the internal motor representation of the observed action can be used for response facilitation, i.e., for triggering the repetition of an observed action that is already in the observer's motor repertoire. Response facilitation is achieved by means of a resonance mechanism (Rizzolatti et al. 1999) in which the motor system of the observer (or the listener) is activated specifically when an appropriate visual (and/or acoustic) stimulus is presented.

Non-human primates may offer an interesting model to test this hypothesis. Recently, we experimentally targeted a behaviour that is particularly sensitive to social input: eating behaviour. In a series of behavioural experiments carried out in macaques (Ferrari et al. in press) we tested the hypothesis, based on the mirror system function, that the observation and hearing of eating actions activates the motor programs of similar actions, thus facilitating their execution. Monkeys that were fed and had left over food in their cages increased their feeding behaviour when they observed (experiment 1), or just heard (experiment 2), other individuals eating (Figure 2). In contrast, the sound (control) of ripping paper did not elicit any eating behaviour in the listener (experiment 3). Which is the function of this synchrony of monkey feeding behaviour? Since in primates feeding is characterized by being primarily social, we speculated that feeding activities of macaque monkeys necessitate social sensitiveness aimed at tuning individuals' own behaviour with that of group members. Behavioural coordination, i.e., doing the same things at the same time (Coussi-Korbel & Fragaszy 1995) has undoubted advantages; for example, group cohesiveness (that is an effective anti-predator behavioural strategy) which is promoted by timing similar activities with others.

Another form of intersubjectivity is early imitation that was firstly described by Meltzoff and Moore in human infants (1977). This and other studies clearly showed that human infant can imitate facial gestures made by an adult, such as mouth opening, tongue protrusion and lips protrusion (Kugiumutzakis 1998, 1999; Meltzoff & Gopnik 1993). How can it be possible to imitate facial gestures if the infant cannot see his/her face? How can he/she match his/her face with that of the model? What happens is the translation of the personal perspective of the demonstrator into the infant body perspective. Following the same reasoning on the resonance mechanism of the motor system underpinned by the mirror neurons functioning, it is possible to postulate that in early imitation neonates' motor systems can innately respond specifically to the experimenter gesture without having a visual feedback of their own face. This direct link between observed and executed acts, embedded in the mirror system may have important implications for the development of intersubjectivity. According to Meltzoff and colleagues (1992, 2002) early imitation can be an important tool to learn about persons and about objects and to distinguish the identity of other people and thus a way to enter into a personal relationship with others.

Studies on nonhuman primates may help to better understand possible functions of early imitation and to track a possible evolutionary path towards an emergence of this behaviour. Similarly to humans, also in chimpanzee it has been reported a case of facial imitation that takes place very early after birth (Myowa 1996; Myowa et al. 2004). It lasts two months before disappearing. These authors suggested that neonatal imitation in chimpanzees enables newborns to orient preferentially to the conspecifics' face. Although still anecdotal, we have observed

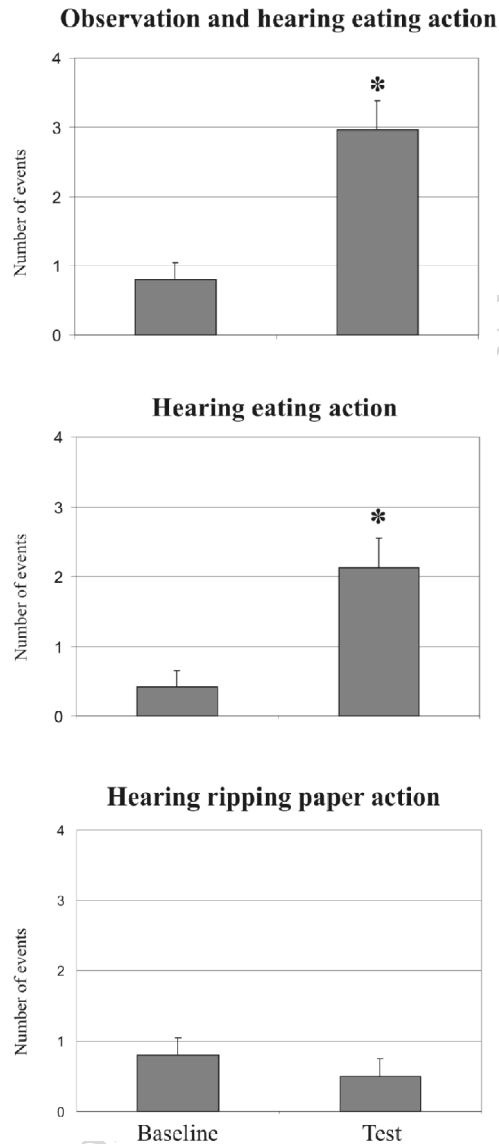


Figure 2. Mean number of instantaneous eating sample points scored during baseline and test period in ten pig-tailed macaques (*Macaca nemestrina*). Each individual contributed with the averaged value of its three sessions. During the *baseline* period the demonstrator was visible to the observer (only in experiment 1) but could not eat any food. During the *test* period the stimulus (the sound or the vision of a monkey eating food) was introduced (A) Experiment 1 (monkey heard and observed another individual eating), (B) Experiment 2 (monkey heard another individual eating), and (C) Experiment 3 (monkey heard ripping paper sound). Asterisks indicate significant differences between test and baseline period scan samples ($p < 0.05$, Wilcoxon test). From Ferrari et al. (in press).

a similar phenomenon in an infant macaque at the age of one week. Using a methodology similar to that adopted by Meltzoff and Moore (1977) we tested the behavioural response specificity of the infant macaque to human and facial and hand gestures. The facial and hand gestures used as stimuli were: mouth opening, lips protrusion, tongue protrusion and hand opening. The infant macaque was tested at the age of 1 and 2 weeks. At the age of 1 week, this infant macaque seemed to imitate tongue protrusion, lipsmacks and mouth openings when it saw them performed by a human experimenter (see Figure 3). Although, still preliminary, these findings suggest that macaques may possess such imitative capacity very soon after birth (i.e. in the first week of life), which, however, tends to disappear very soon. Although data on nonhuman primates are very scarce, it is clear that human early imitation is not a unique feature of the human being but has evolved probably from other related non-human primates. The fact that the type of gestures imitated are usually related to affiliate meanings seems to suggest that in primates the need to establish a deep relation (not just in term of attachment but also in term of different forms of intersubjectivity) between two individuals, typically the mother and the infant, could have been a crucial evolutionary force. Furthermore, what the data on early imitation seems to suggest is that in some species of primates the newborn is capable of tuning his/her behaviour with that observed by another individual. The sensory-motor system is already set to be coordinated with someone else's experience in a participatory sense. This 'alter-centred participation' is one of the tenet of the "primary intersubjectivity" model (Bråten 1998). According to this model, in fact, infants have a whole set of capacities to attune their minds with those of others. The result of this attunement is

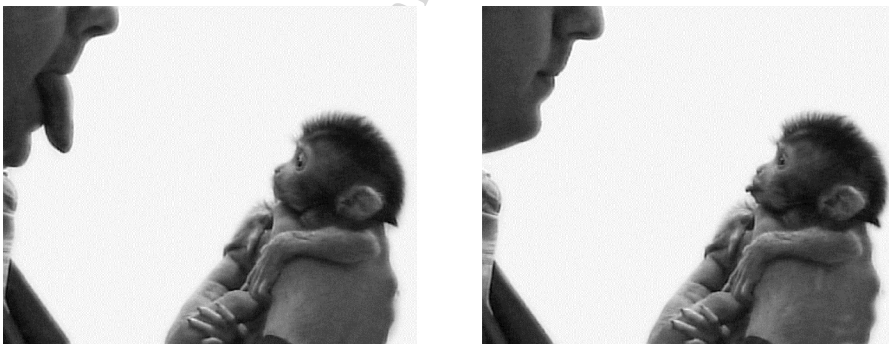


Figure 3. Neonatal imitation of tongue protrusion in a one week old pig-tailed macaque. The two pictures are taken from a videotape. In the left picture is depicted the gesture made by the model that is holding in his hand the infant monkey. The picture on the right has been taken about two seconds after the end of the model's gesture. The gesture made by the model was repeated 7–8 times in a period of 20 seconds. As the monkey protruded its tongue, no other movements (either with the hand or the mouth) were recorded.

that of sharing the first- and the third-person experience. This (probably) innate capacity to enter and participate in other's experience could be served by a neural mechanism such as that of the mirror neurons. One aspect that neuroscience should explore more in depth is whether the mirror neurons matching system is confined to functions such as action understanding or whether the system can be further exploited in the alter-centred participation.

The mirror neuron system and secondary intersubjectivity

Before becoming verbal and symbolic, the infant acquires more complex forms of intersubjectivity. One of these is of utmost importance in the development of the capacity of interacting and sharing experiences with others: understanding intentions.

We will show here that the organization of the motor system may provide a substrate for perceiving/inferring intentions. We will see that for the development of a motor system fully adapted to interact with the physical and inanimate world, it is necessary to intrinsically have a concept of intention for guiding the body in space towards a goal.

Mirror neurons and the understanding of intentions

When an individual starts a movement aimed to attain a goal, such as picking up a pen, he/she has clear in mind what he/she is going to do, for example writing a note on a piece of paper. In this simple sequence of motor acts the final goal of the whole action is present in the agents' mind and is somehow reflected in each motor act of the sequence. The action *intention*, therefore, is set before the beginning of the movements. This also means that when we are going to execute a given action we can also predict its consequences.

Monkeys may exploit the mirror neuron system to optimize their social interactions. At least, the evidence we have collected so far seems to suggest that the mirror neuron system for actions is enough sophisticated to enable its exploitation for social purposes. Recent results by Cisek and Kalaska (2004) show that neurons in the dorsal premotor cortex of the macaque monkey can covertly simulate observed behaviours of others, like a cursor moved to a target on a computer screen, even when the relation between the observed sensory event and the unseen motor behaviour producing it is learned through stimulus-response associations. The hypothesis is that monkeys might entertain a rudimentary form of "teleological stance", a likely precursor of a full-blown intentional stance. This hypothesis extends to the phylogenetic domain the ontogenetic scenario proposed by Gergely and Csibra (2003) for human infants.

But monkeys certainly do not entertain full-blown mentalization. Thus, what makes humans different? At present we can only make hypotheses about the relevant neural mechanisms underpinning the mentalizing abilities of humans that are still poorly understood from a functional point of view. In particular, we do not have a clear neuroscientific model of how humans can understand the intentions promoting the actions of others they observe. A given action can be originated by very different intentions. Suppose one sees someone else grasping a cup. Mirror neurons for grasping will most likely be activated in the observer's brain. A simple motor equivalence between the observed action and its motor representation in the observer's brain, however, can only tell us *what* the action is (it's a grasp) and not *why* the action occurred. Determining why action A (grasping the cup) was executed, that is, determining its intention, can be equivalent to detecting the goal of the still not executed and impending subsequent action (say, drink from the cup).

The view that mirror neurons code the *what* but not the *why* of an action seems to be reversed by recent electrophysiological data. In the inferior parietal lobe (IPL) of the monkey it has been recently described mirror neurons with very interesting properties. They discharge in association with monkey motor acts (grasping) only when they are embedded in a specific action aimed at different goals (Fogassi et al. 2004; Rizzolatti et al. in press; Fogassi et al. in press). For example, a neuron will fire when the monkey grasps a piece of food only if the grasping act is aimed to bring the food into the mouth and not if it is aimed to place the food into a container. Thus, these neurons code the same motor act differently depending on the final action goal. Fogassi and colleagues (2004) proposed that the motor properties of these mirror neurons and of other motor neurons found in the IPL could be that of facilitating the fluidity of an action in which different motor acts follow one the other. Single motor acts are dependent to each other as they participate to the global goal of an action, thus forming pre-wired intentional chains, in which each next motor act is facilitated by the previously executed one.

The visual response of some of these mirror neurons is similar to their motor response. In fact, they discharged differentially depending on whether the observed grasping was followed by bringing to the mouth or by placing. Note that the neurons' activation is present before the monkey observes the experimenter starting the second motor act (bringing food to the mouth or placing it into the container). This new property of parietal mirror neurons, suggest that in addition to recognizing the goal of the observed motor act, they discriminate identical motor acts according to the action in which these acts are embedded. This would allow the monkey to *predict* what is the goal of the observed action and, thus, to "read" the intention of the acting individual.

The mechanism of intention understanding just described appears to be rather simple. Depending on which motor chain is activated, the observer is going to have an internal representation of what, most likely, the action agent is going to do.

This view is corroborated by a recent fMRI study carried out in healthy human subjects (Iacoboni et al. 2004) showing that premotor mirror neurons-related areas not only code the “what” of an action but also its “why”, that is, the intention promoting it. Detecting the intention of Action A is equivalent to predict its distal goal, that is, the goal of the subsequent Action B.

The statistical frequency of action sequences (the detection of what most frequently follows what), as they are habitually performed or observed in the social environment, can therefore constrain preferential paths of inferences/predictions. As hypothesized above, this can be accomplished by chaining different populations of mirror neurons coding not only the observed motor act, but also those that in a given context would normally follow. Ascribing intentions would therefore consist in predicting a forthcoming new goal.

Mirroring emotions and sensations

Emotions constitute one of the earliest ways available to the individual to acquire knowledge about its situation, thus enabling to reorganize this knowledge on the basis of the outcome of the relations entertained with others. The coordinated activity of sensory-motor and affective neural systems results in the simplification and automatization of the behavioural responses that living organisms are supposed to produce in order to survive. The integrity of the sensory-motor system indeed appears to be critical for the recognition of emotions displayed by others (see Adolphs 2003; Adolphs et al. 2000), because the sensory-motor system appears to support the reconstruction of what it would feel like to be in a particular emotion, by means of simulation of the related body state. The implication of this process for empathy should be obvious.

A recently published functional Magnetic Resonance Imaging (fMRI) study showed that experiencing disgust and witnessing the same emotion expressed by the facial mimicry of someone else, both activate the same neural structure – the anterior insula – at the same overlapping location (Wicker et al. 2003). This suggests, at least for the emotion of disgust, that the first- and third-person experiences of a given emotion are underpinned by the activity of a shared neural substrate. Thus, it is the activation of a neural mechanism shared by the observer and the observed to enable direct experiential understanding.

Similar to emotions, also the tactile dimension can be intimately related to the interpersonal dimension. New empirical evidence suggests that the first-person experience of being touched on one’s body activates the same neural networks activated by observing the body of someone else being touched (Keysers et al. 2004).

Within SII-PV, a multimodal cortical region, there is a localized neural network similarly activated by the self-experienced sensation of being touched, and the perception of an external tactile relation.

The double pattern of activation of the same brain region suggests that our capacity to experience and directly understand the emotional and tactile experience of others could be mediated by embodied simulation, that is, by the externally triggered activation of some of the same neural networks underpinning our own emotion and tactile sensations (see Gallese in press).

Conclusion

In the present chapter we propose that mirror neurons and mirror-related mechanisms here described may represent the neurobiological grounding for the expression of some forms of primary and secondary intersubjectivity. These mechanisms allow individuals to participate in another's action, feeling or emotion through a preferential access of the visual information about the outside social world to our sensorimotor experience. The mirror neuron systems and the other non-motor mirroring neural clusters in our brain represent *one particular* sub-personal instantiation of embodied simulation. With this mechanism we do not just "see" an action, an emotion, or a sensation. Side by side with the sensory description of the observed social stimuli, internal representations of the body states associated with these actions, emotions, and sensations are evoked in the observer, 'as if' he/she would be doing a similar action or experiencing a similar emotion or sensation.

According to this perspective, social cognition is not *only* explicitly reasoning about the contents of someone else's mind. Our brains, and those of other primates, appear to have developed a basic functional mechanism, embodied simulation, which gives us an experiential insight of other minds.

We also elucidated the possible link between the organization of the motor system and its capacity to generate internal representations of what the agent is going to do. In fact, the motor neurons in the parietal cortex seem to be organized in chains that code different motor acts which are dependent to each other as they participate to the global overarching goal of an action. By means of embodied simulation, the activation of these chains during the observation of motor acts of others determines the activation in the observer's brain of the final goal of the action. Thus, mirror neurons appear to be a suitable mechanism not only for action understanding but also for the detection of the intentions promoting the behaviour of others. In other terms, as previously hypothesized (Gallese & Goldman 1998), it could be at the basis of basic forms of mind reading.

The shareability of the phenomenal content of the intentional relations of others, by means of the shared neural underpinnings, produces intentional at-

tunement (cf. Fogassi et al. 2005). Intentional attunement, in turn, by collapsing the others' intentions into the observer's ones, produces the peculiar quality of familiarity we entertain with other individuals. This is what "being empathic" is about (see Gallese in press). By means of a shared neural state realized in two different bodies that nevertheless obey to the same functional rules, the "objectual other" becomes "another self".

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