Embodied simulation: From neurons to phenomenal experience

VITTORIO GALLESE

Dipartimento di Neuroscienze, Sezione di Fisiologia Università di Parma Italy
(E-mail: vittorio.gallese@unipr.it)

Abstract. The same neural structures involved in the unconscious modeling of our acting body in space also contribute to our awareness of the lived body and of the objects that the world contains. Neuroscientific research also shows that there are neural mechanisms mediating between the multi-level personal experience we entertain of our lived body, and the implicit certainties we simultaneously hold about others. Such personal and body-related experiential knowledge enables us to understand the actions performed by others, and to directly decode the emotions and sensations they experience. A common functional mechanism is at the basis of both body awareness and basic forms of social understanding: embodied simulation. It will be shown that the present proposal is consistent with some of the perspectives offered by phenomenology.

Key words: body-image, body-schema, embodied simulation, experiential knowledge, intentional attunement, mirror neurons, shared manifold

Introduction

> . . . we are saying that the body, in so far as it has 'behaviour patterns', is that strange object which uses its own parts as a general system of symbols for the world, and through which we can consequently 'be at home' in that world, 'understand' it and find significance in it (Merleau-Ponty 1962, p. 237)

How does our brain model our acting body? And how does it model the acting body of other individuals? What is the relevance of these bodily models/representations for our capacity to phenomenally experience our own acting body and the acting body of others? In the present article I will try to address these issues, by referring to empirical neuroscientific research carried out both on monkeys and humans. This will come in two parts: In the first part I will illustrate a parieto-premotor cortical circuit providing not only the neural correlate for the unconscious mapping of our acting body in space *but also* for its conscious awareness. In the second part I will show that other neural circuits, responsible for guiding our actions in the world and mapping the emotions and sensations we experience, are also used to interpret and directly understand the meaning of the actions performed by others and of the emotions and sensations they experience. I will show throughout the paper that many of the neuroscientific results here reviewed and the theoretical considerations they promote are consistent with some of the perspectives offered

by phenomenology. I will conclude by proposing that a common functional mechanism is at the basis of both body awareness and basic forms of social understanding: embodied simulation.

Awareness of body and space

When I stretch my arm to reach for a cup of coffee placed on the desk, my hand, regardless of its starting position, reaches for and grasps the cup without any conscious effort. In order to correctly transport my hand to the desired location, my motor system needs to know where my hand was located before movement onset. Due to proprioception, this capacity does not require visual information about where my hand actually is. However, if my somatosensory system is not working properly, as in the case of deafferented patients, the only solution available to my brain is to visually monitor where my hand is and where it is supposed to go. According to the seminal distinction introduced by Head and Holmes (1911–1912), what peripherally deafferented patients suffer is a disturbance of their "body schema." The body-schema, according to this definition, is therefore an *unconscious* body map, which enables us to program and monitor the execution of actions with the different body parts.

In sharp contrast with the body-schema, stands the notion of a "body image," introduced by Schilder (1935) as a *conscious perception* of our own body. The dichotomy between the unconscious and the conscious dimensions provides the coordinates still in use in the current literature to characterize how the brain maps our body. This dichotomy, however, seems to presuppose a clear-cut division of labor between neural systems operating below and above the level of consciousness. As it will become clearer in the course of this paper, this distinction might turn out to be over simplistic.

The neuroscientific evidence accumulated during the last two decades has deeply changed our views about sensory-motor integration and its role in cognition. It has been shown that cortical premotor areas are endowed with sensory properties. They contain neurons that respond to visual, somatosensory, and auditory stimuli. Posterior parietal areas, traditionally considered to process and associate purely sensory information, indeed turned out to also play a major role in motor control. The premotor and parietal areas, rather than having separate and independent functions, are neurally integrated not only to control action, but also to serve the function of building an integrated representation of (a) actions together with (b) objects acted on and (c) locations toward which actions are directed. In particular, these multi-modal functions have been described within three parallel parietal-premotor cortical networks: F5ab-AIP, F4-VIP, and F5c-PF-PFG (see Gallese and Lakoff 2005). I will confine myself here to a brief characterization of the F4-VIP network.

The cortical circuit formed by area F4, which occupies the posterior sector of the ventral premotor cortex of the macaque monkey, and area VIP, which occupies the fundus of the intraparietal sulucus, is involved in the *organization of head and arm actions in space*. Single neuron studies showed that in area VIP there are two main classes of neurons responding to sensory stimuli: purely visual neurons and bimodal, visual and tactile neurons. Bimodal VIP neurons respond independently to both visual and tactile stimuli. Tactile receptive fields are located predominantly on the face. Tactile and visual receptive fields are usually in "register," that is, the visual receptive field encompasses a three-dimensional spatial region (peripersonal space) around the tactile receptive field. Some bimodal neurons are activated preferentially or even exclusively when 3D objects are moved towards or away from the tactile receptive field. About thirty percent of VIP neurons code space in reference to the monkey's body. There are also neurons that have hybrid receptive fields. These receptive fields change position when the eyes move along a certain axis, but remain fixed when the eyes move along another axis (Duhamel et al. 1997).

Consistent with the single neuron data, are the results of lesion studies. Selective electrolitic lesion of area VIP in monkeys determines mild but consistent contralesional neglect for peripersonal space. No changes were observed in ocular saccades, pursuit and optokinetik nistagmus. Tactile stimuli applied to the contralesional side of the face also failed to elicit orienting responses. (Duhamel, personal communication).

Single neurons studies showed that most F4 neurons discharge in association with monkey's active movements (Gentilucci et al. 1988). The movements more represented are head and arm movements, such as head turns and reaching. Most F4 neurons respond to sensory stimuli. As neurons in VIP, F4 sensory-driven neurons can be subdivided into two classes: unimodal, purely sensory neurons, and bimodal, somatosensory and visual neurons (Gentilucci et al. 1988; Fogassi et al. 1992, 1996). Tactile receptive fields, typically large, are located on the face, chest, arm and hand. Visual receptive fields are also large. They are located in register with the tactile ones, and similarly to VIP, confined to the peripersonal space (Gentilucci et al. 1983, 1988; Fogassi et al. 1992, 1996; Graziano et al. 1994). Recently, trimodal neurons responding also to auditory stimuli were described in F4 (Graziano et al. 1998).

Studies of the visual properties of F4 neurons showed that in most F4 neurons the receptive fields do not change position with respect to the observer's body when the eyes move (Gentilucci et al. 1983; Fogassi et al. 1992, 1996; Graziano et al. 1994). This indicates that the visual responses of F4 do not signal positions on the retina, but positions in space relative to the observer. Interestingly, the spatial coordinates of the visual receptive fields are anchored to different body parts, and not to a single reference point, as suggested on the basis of psychological experiments by some motor theorists. Visual receptive fields located around a certain body part (e.g., arm) move when that body

part is moved (Graziano et al. 1997). Allocentric coding was also tested and contrasted with egocentric coding: in all tested neurons the receptive field organization was found to be coded in egocentric coordinates (Fogassi et al. 1996 a,b).

Empirical evidence in favor of the simulation-based motor nature of peripersonal space derives from the properties of F4 neurons. In principle there are two main possibilities on what these neurons code. The first is that they code space "visually". If this is so, given a reference point the neurons should signal the location of objects by using a Cartesian or some other geometrical system. The alternative possibility is that the discharge of neurons reflects a potential, simulated motor action directed towards a particular spatial location. This simulated potential action would create a motor space. When a visual stimulus is presented, it evokes directly the simulation of the congruent motor schema which, regardless of whether the action is executed or not, maps the stimulus position in motor terms.

Arguments in favor of the visual hypothesis are the tight temporal link between stimulus presentation and the onset of neural discharge, the response constancy, and the presence of what appears to be a visual receptive field. If, however, there is a strict association between motor actions and stimuli that elicit them, it is not surprising that stimulus presentation determines the effects just described. More direct evidence in favor of a motor space came from the study of properties of F4 neurons in response to moving stimuli. According to the visual hypothesis, each set of neurons, when activated should specify the object location in space, regardless of the stimulation's temporal dimension. A locus 15 cm from the tactile origin of the visual receptive field should remain 15 cm from it regardless of *how* the object reaches this position. The spatial map, as expressed by receptive field organization, should be basically static. In contrast, in the case of motor space, because time is inherent to movement, the spatial map may have dynamic properties and may vary according to the change in time of the object's spatial location. The experiments of Fogassi et al. (1996) showed that this is indeed the case. The visual receptive field extension of F4 neurons increases in depth when the speed of an approaching stimulus increases.

The notion that spatial awareness is linked to movement has a long history. Particularly interesting is the attempt of Von Helmoltz (1896) to substitute the Kantian notion that space is an "a priori" with the notion that this "a priori" is generated by exploration behavior. Indeed, as it has been argued elsewhere (see Rizzolatti et al. 1997), a strong support to the notion that spatial awareness derives from motor activity is the demonstration of the existence of peri-personal space. From a purely sensory point of view, there is no principled reason that eyes with normal refraction should select light stimuli coming exclusively from a space sector located around the

body of the perceiver. Light stimuli arriving from far or from near should be equally effective. However, if we consider that peripersonal stimuli occupy the space where the targets of the actions performed by hands and mouth are mostly located, it becomes clear why space is mapped in motor terms.

It is interesting to note the closeness of the view emerging from single-neuron recordings, and the philosophical perspective offered by phenomenological philosophers on space perception (see Zahavi 2002). As Merleau-Ponty (1962, p. 243) wrote, space is ". . . not a sort of ether in which all things float.... The points in space mark, in our vicinity, the varying range of our aims and our gestures." Furthermore, It is interesting to note that Husserl wrote that every thing we see, we simultaneously also see it as a tactile object, as something which is directly related to the alive body, but not by virtue of its visibility (Husserl 1989). The "tactile lived body," in particular, provides the constitutive foundation of our cognitive and epistemic self-referentiality. The perspectival spatial location of our body provides the essential foundation to our determination of reality. The body entertains a dual reality of spatial externality and internal subjectivity (Husserl 1925, p. 197). But in contrast to what Husserl considered the *physiological* definition of the body, as a material object, contemporary neurophysiological research suggests that the sensory-motor system is also responsible for the phenomenal awareness of its relations with the world.

Why is action important in spatial awareness? Because what integrates multiple sensory modalities within the F4-VIP neural circuit is action simulation. Vision, sound and action are parts of an integrated system; the sight of an object at a given location, or the sound it produces, automatically triggers a "plan" for a specific action directed toward that location. What is a "plan" to act? It is a simulated potential action.

The characterization so far provided of this cortical network would seem at first sight to be fully consistent with a particular aspect of the body-schema, that is, the control of body actions within peripersonal space. If, however, we consider the results of lesion of this network, a different picture emerges. Unilateral lesion of the ventral premotor cortex of the monkey, including area F4, produces two series of deficits: motor deficits and perceptual deficits (Rizzolatti et al. 1983; see also Rizzolatti, Berti and Gallese 2001). Motor deficits consist in a reluctance to use the contralesional arm, spontaneously or in response to tactile and visual stimuli, and in a failure to grasp with the mouth food presented contralateral to the side of the lesion. Perceptual deficits concern neglect of the contralesional peripersonal space, and of the personal (tactile) space. A piece of food moved in the contralesional space around the monkey's mouth does not elicit any behavioral reaction. Similarly, when the monkey is fixating a central stimulus, the introduction of food contralateral to

the lesion is ignored. In contrast, stimuli presented outside the animal's reach (far space) are immediately detected.

Neglect in humans occurs after lesion of the IPL and, less frequently, following damage of the frontal lobe, and in particular following lesions of area 6, 8, and 45 (see Bisiach and Vallar 2000). The most severe neglect in humans occurs after lesion of the right IPL. In the full-fledged unilateral neglect, patients may show a more or less complete deviation of the head and eyes towards the ipsilesional side. Routine neurological examination shows that patients with unilateral neglect typically fail to respond to visual stimuli presented in the contralesional half field and to tactile stimuli delivered to the contralesional limbs. As in monkeys, also in humans neglect may selectively affect the extrapersonal and the peripersonal space. In humans, this dissociation was first described by Halligan and Marshall (1991). They examined a patient with severe neglect using a line bisection task. In this task the subject is usually required to mark the midpoint of a series of lines scattered all over a sheet of paper. The task was executed in the near space and in the space beyond hand reaching distance using a laser pen that the patient held in his right hand. The results showed that when the line was bisected in the near space the midpoint mark was displaced to the right, as typically occurs in neglect patients. However, the neglect dramatically improved or even disappeared when the testing was carried out in the far space. A similar dissociation was reported by Berti and Frassinetti (2000). Other authors described the opposite dissociation: severe deficits in tasks carried out in the extrapersonal space, slight or no deficit for tasks performed in the peripersonal space (see Shelton et al. 1990; Cowey et al. 1994, 1999). The lesions causing neglect in humans are usually very large, thus while the findings of separate systems for peripersonal and extrapersonal space are robust and convincing, any precise localization of the two systems in humans is at the moment impossible.

In conclusion, lesions of IPL and its frontal targets both in monkeys and humans determine body awareness deficits. Furthermore, it must be stressed that not only does IPL appear to play a fundamental role in body and spatial awareness, but it is also necessary for the *awareness of the quality of objects* presented within peripersonal space. Evidence in favor of this point of view comes from a series of clinical and neuropsychological studies. Marshall and Halligan (1988) reported the case of a lady who, due to a severe visual neglect, explicitly denied any difference between the drawing of an intact house and that of the same house when burning, if the relevant features for the discrimination were on the neglected side. However, when forced to choose the house where she would prefer to live, she consistently choose the intact one, showing in this way an implicit knowledge of the content she was unable to report. Berti and Rizzolatti (1992) confirmed these findings in a systematic way. In their experiments patients with severe unilateral neglect were asked to respond as fast as possible to target stimuli presented within the intact visual

field by pressing one of two keys according to the category of the target (fruits and animals). Before showing these stimuli, pictures of animals and fruits were presented to the neglected field as priming stimuli. The patients denied seeing these priming stimuli. Yet, their responses to the stimuli shown in the intact field were facilitated by the primes. This occurred not only in "highly congruent conditions", that is when the prime stimulus and the target were physically identical (e.g. a dog), but also when prime and stimulus constituted two elements of the same semantic category, though physically dissimilar (e.g. a dog and an elephant).

These findings demonstrate that neglect patients are able to process stimuli presented within the neglected field up to a categorical semantic level of representation. However, they are not aware of them in the absence of IPL processing. This implies that the parieto-frontal sensorimotor circuits must be intact for achieving awareness even of those stimuli, such as fruits or animals, that are analyzed mostly in the ventral stream.

Lesions of sensori-motor circuits, whose primary function is that of controlling movements of the body or of body parts towards or away from objects, produce deficits that do not exclusively concern the capacity to orient towards objects or to act upon them. These lesions produce also deficits in body, space, and object awareness.

The shared body of interpersonal relationships

Folk psychology is a way to describe how our mind is related to reality. According to folk psychology, thought is referential and the content of mental representations is described in terms of intentions, desires, and beliefs. Within a *social* cognitive level of description, according to folk psychology, we hold intentions, desires, and beliefs about other individuals, whose intentions, desires, and beliefs constitute the object of our social cognition. Classic cognitivism and some quarters in philosophy of mind grant ontological status to folk psychological notions like intention, desire, and belief, and provide an impressively detailed analytic description of the distinctive functional features characterizing them. There is one particular aspect of this classic model of the mind that I take to be particularly relevant to a discussion of the neural correlates of social cognition. This aspect concerns the analysis of intention and its relationship with social perception.

Cognitive scientists, philosophers, and neuroscientists have – often jointly – recently taken up the challenge of a serious project of naturalization of social intentionality. According to folk psychology, when we perceive other acting individuals we translate the perception of their actions into the intentions, desires and beliefs that likely caused them. It has been emphasized that intentions and perceptions have different directions of fit (see Searle 1992;

see also Jacob and Jeannerod 2003). Intentions would require the world to conform to the goals set by a volitional self. Conversely, perceptions would require the mind to conform to the objectively given world. These opposite relational directions actually reverse, when analyzed in terms of causation. Intentions reveal a mind-to-world causal relationship, while in perceptions the world causes the mind to instantiate particular representational states.

A neurobiologically plausible naturalization of social cognition thus entails the search for neural states capable of mapping intentions on perceptions within an integrated informational content. Intentions must henceforth be coded in the same representational format of their perception.

The first obstacle is represented by the ontological commitments of our naturalizing epistemic strategy. If folk psychological concepts have a distinct ontological status, their naturalization necessarily implies the search for a neural functional characterization of the same concepts. The risk of this strategy is to flatten the naturalization project to a mere neural correlation enterprise, often defined according to neural maps whose topology is normatively related to the basic ontological commitments of the same folk psychological concepts they should underpin. (e.g., see the vast literature on the neural correlates of the Theory of Mind Module). The whole enterprise seems to suffer of circularity. Hence I doubt that by applying this analysis to the study of social cognition we will ever be close to integrating the folk psychological and the neuroscientific levels of description within a coherent and biologically plausible naturalized framework. Let us see why.

Within our social world we perceive the actions performed by others, and we recognize and understand their meaning. These "social perceptions", according to the classic account, are mapped with a mind-to-world direction of fit. But the objects of our cognitive social perceptions are the intentional relations of other minds. We have henceforth a mind-to-mind direction of fit. As it will become clearer further on in the paper, the mind/world distinction can be better understood in terms of a mereological relation.

Our social mental skills enable us to successfully retrieve the mental contents of others. Sometimes we misrepresent them, hence misunderstanding others. Most of the time, though, we are pretty good at understanding the goal of others' behavior, why the goal was set, and on the basis of which previous elements the goal was set as such. We do it effortlessly and continuously during our daily social interactions. How is that accomplished? The dominant view in cognitive science is to clarify the formal rules structuring a solipsistic mind. Less attention has been devoted to investigate what triggers the sense of identity that we experience with the multiplicity of "other selves" populating our social world. Is the solipsistic type of analysis, inspired by folk-psychology, the best explanatory approach? In particular,

is it doing full justice to the phenomenal aspects of our social intentional relations?

As human beings, we do not only mentally entertain an "objective" account of the behaviors constituting the social world in which we live. Beyond phenomenally experiencing the external, objective nature of an observed action, and viewing it as something displayed and acted by an external biological object, we also experience its goal-directedness or intentional character, similarly to when we experience ourselves as the willful conscious agents of an ongoing behavior. From a first-person perspective, our dynamic social environment appears to be populated by volitional agents capable of entertaining, similarly to us, an agentive intentional relation to the world. We experience other individuals as *directed* at certain target states or objects, similarly to how we experience ourselves when doing so.

The same dual perspective is at work when witnessing the emotions and sensations experienced by others. We can provide an "objective" description of these emotions or sensations. When explicitly asked to recognize, discriminate, parameterize, or categorize the emotions or sensations displayed by others, we exert our cognitive operations by adopting a third-person perspective, aimed exactly at *objectifying* the content of our perceptions. The overall goal of these cognitive operations is the deliberate categorization of an external state of affairs.

However, when we are involved on-line with social transactions, we experience a totally different attitude toward the objects of our perceptions. There is actually a shift of the object of our intentional relation. We are no longer directed to the content of a perception in order to categorize it. We are just *attuned to the intentional relation displayed by someone else*. In contrast to Mr. Spock, the famous character of the Star Trek saga, our social mental skills are not confined to a declarative third-person perspective. We are not alienated from the actions, emotions and sensations of others, because we entertain a much richer and affectively nuanced perspective of what other individuals do, experience, and feel. What makes this possible is the fact that *we own* those same actions, emotions, and sensations.

To naturalize social intentionality we should perhaps follow an alternative route. The alternative strategy I suggest here is a bottom-up characterization of the non-declarative and non-conceptual contents of social cognition. It consists in investigating the neural basis of our capacity to be attuned to the intentions of others. By means of *intentional attunement*, "the other" is much more than a different representational system; it becomes a *person*, like us. The advantage of such an epistemological approach is that it generates predictions about the intrinsic functional nature of our social cognitive operations that cut across, and neither necessarily depend on, nor are subordinate to any specific cognitive mind ontology, including that of Folk Psychology.

Action understanding

Our social world is inhabited by a multiplicity of acting individuals. Much of our social competence depends on our capacity for understanding the meaning of the actions we witness. These actions basically pertain to two broad categories. The first is the category of transitive, object-related actions, like grasping a coffee mug, picking up a phone, biting an apple, or kicking a football. The second category of social actions is that of intransitive, expressive or deictic actions, like sending kisses, uttering words, or pointing to a person or location in space. What makes our perception of both types of actions different from our perception of the inanimate world is the fact that there is something shared between the first and third person perspective of the former events; the observer and the observed are both human beings endowed with a similar brain-body system making them act alike (Gallese 2001).

The discovery of mirror neurons has triggered new perspectives on the neural mechanisms at the basis of action understanding. I deal first with transitive actions.

The understanding of object-related actions

About ten years ago a new class of premotor neurons discharging 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 was discovered in the macaque monkey brain. These neurons were called "mirror neurons" (Gallese et al. 1996; Rizzolatti et al. 1996a; see also Gallese 2000, 2001, 2003a,b, 2005). Neurons with similar properties were later discovered in a sector of the posterior parietal cortex reciprocally connected with area F5 (PF mirror neurons, see Gallese et al. 2002a).

The observation of an object-related action leads to the activation of the same neural network active during its actual execution. Action observation causes in the observer the automatic simulated re-enactment of the same action. We proposed that this mechanism could be at the basis of an implicit form of action understanding (Gallese et al. 1996; Rizzolatti et al. 1996a; see also Gallese 2000, 2003b; Gallese et al. 2002a,b).

The relationship between action understanding and action simulation is even more evident in the light of the results of two more recent studies carried out in our laboratory. In the first series of experiments, F5 mirror neurons were tested in two conditions. In the first condition the monkey could see the entire action (e.g. a hand grasping action); in the second condition, the same action was presented, but its final critical part, that is, the hand-object interaction, was hidden. Therefore, in the hidden condition the monkey only "knew" that the target object was present behind the occluder. The results showed that more

than half of the recorded neurons responded also in the hidden condition (Umiltà et al. 2001). These results seem to suggest that inferences about the goals of the behavior of others appear to be mediated by the activity of motor neurons coding the goal of the same action in the observer's brain. Out of sight is not "out of mind" just because, by simulating the action, the gap can be filled.

Some transitive actions are characteristically accompanied by a specific sound. Often this particular sound enables us to understand what is going on even without any visual information about the action producing the sound. The perceived sound has the capacity to make an invisible action inferred, and therefore present and understood.

It was shown that a particular class of F5 mirror neurons, "audio-visual mirror neurons", discharge not only when the monkey executes or observes a particular type of noisy action (e.g. breaking a peanut), but also when it just listens to the sound produced by the action (see Kohler et al. 2002; Keysers et al. 2003).

These "audio-visual mirror neurons" not only respond to the sound of actions, but also discriminate between the sounds of different actions. The actions, whose sounds maximally trigger the neurons' discharge when heard, are those that also produce the strongest response when observed or executed. The activation of the premotor neural network normally controlling the execution of action "A" by sensory information related to the same action "A," be it visual or auditory, can be characterized as simulating action "A".

The multi-modally driven simulation of action goals instantiated by neurons situated in the ventral pre-motor cortex of the monkey, instantiates properties that are strikingly similar to the symbolic properties so characteristic of human thought. The similarity with conceptual content is quite appealing: the same conceptual content ("the goal of action A") results from a multiplicity of states subtending it, sounds, observed and executed actions. These states, in turn, are subtended by differently triggered patterns of activations within a population of "audio-visual mirror neurons".

The *action simulation* embodied by audiovisual mirror neurons is indeed reminiscent of the use of predicates. The verb 'to break' is used to convey a meaning that can be used in different contexts: "Seeing someone breaking a peanut", "Hearing someone breaking a peanut", "Breaking a peanut". The predicate, similarly to the responses in audiovisual mirror neurons, does not change depending on the context to which it applies, nor depending on the subject/agent performing the action. All that changes is the context the predicate refers to (Gallese 2003c; see also Gallese and Lakoff 2005).

The general picture conveyed by these results is that the sensory-motor integration supported by the premotor-parietal F5-PF mirror matching system instantiates simulations of transitive actions utilized not only to generate and control goal-related behaviors, but also to map the goals and purposes of

others' actions, by means of their simulation. This account doesn't entail an explicit declarative format. It is meaningful *and* non-propositional.

What is the import of these data for our understanding of *human* social cognition? Several studies using different experimental methodologies and techniques have demonstrated in humans also the existence of a similar mirror system, matching action perception and execution (see Fadiga et al. 1995; Grafton et al. 1996; Rizzolatti et al. 1996b; Cochin et al. 1998; Decety et al. 1997; Hari et al. 1999; Iacoboni et al. 1999; Buccino et al. 2001). In particular, it is interesting to note that brain imaging experiments in humans have shown that 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 (Grafton et al. 1996; Rizzolatti et al. 1996b; Decety et al. 1997; Decety and Grèzes 1999; Iacoboni et al. 1999; Buccino et al. 2001).

The Understanding of Intransitive Actions

The macaque monkey ventral premotor area F5 also contains neurons related to mouth actions. These neurons largely overlap with hand-related neurons; however, in the most lateral part of F5, mouth-related neurons tend to be prevalent. We recently explored the most lateral part of area F5 where we described a population of mirror neurons mostly related to the execution/observation of mouth related actions (Ferrari et al. 2003). The majority of these neurons discharge when the monkey executes and observes transitive object-related ingestive actions, such as grasping, biting, or licking. However, 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 mirror neurons", Ferrari et al. 2003). These actions are lip-smacking, lips or tongue protrusion. A behavioral study showed that the observing monkeys correctly decoded these and other communicative gestures performed by the experimenter in front of them, because they elicited congruent expressive reactions (Ferrari et al. 2003). It is therefore plausible to propose that communicative mirror neurons might constitute a further instantiation of a simulation-based social heuristic.

A recent brain imaging study, in which human participants observed mouth actions performed by humans, monkeys and dogs (Buccino et al. 2004), further corroborates this hypothesis. The observed mouth actions could be either transitive, object-directed actions, like a human, a monkey, or a dog biting a piece of food, or intransitive communicative actions, like human silent speech, monkey lip-smacking, and dog barking. The results showed that the observation of all biting actions led to the activation of the mirror circuit, encompassing the posterior parietal and ventral premotor cortex (Buccino et al. 2004).

Interestingly, 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, the premotor 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 exstrastriate 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 likely categorized on the basis of their visual properties.

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 silent speech-related lip movements enhanced the size of the motor-evoked potential in lip muscles. This effect was lateralized to the left hemisphere. Consistent with the brain imaging data of Buccino et al. (2004), the results of Watkins et al. (2003) show that the observation of communicative, speech-related mouth actions, facilitate the excitability of the motor system involved in the production of the same actions. Again, we have evidence that embodied simulation mediates the decoding of social meaningful actions.

Action understanding as action simulation

When a given action is planned, its expected motor consequences are forecast. This means that when we are going to execute a given action we can also predict its consequences. This prediction is the computational result of the action model. Through a process of "equivalence" between what is acted and what is perceived, given its shared and overlapping sub-personal neural mapping, this information can also be used to predict the consequences of actions performed by others. This equivalence – underpinned by the activity of mirror neurons – is made possible by the fact that both predictions (of our actions and of others' actions) are simulation (modeling) processes. The same functional logic that presides over self-modeling is employed also to model the behavior of others: to perceive an action is equivalent to internally simulating it. This enables the observer to use her/his own resources to penetrate the world of the other by means of a direct, automatic, and unconscious process of motor simulation. Such simulation processes automatically establish a direct link between agent and observer, in that both are mapped in a neutral fashion. The agent parameter is specified, but not its specific filler, which is indeterminate. Mirror neurons constitutively map an agentive relation; the mere observation of an object not acted upon indeed does not evoke any response (Gallese et al.

1996). It is just the agentive relational specification that triggers the mirror neurons' response. The fact that a *specific agent* is not mapped doesn't entail that an agentive relation is not mapped, but simply that the agent parameter can either be oneself or the other.

As we have seen, in humans as in monkeys, action observation constitutes a form of action simulation. This kind of simulation, however, is different from the simulation processes occurring during visual and motor imagery. Action observation *automatically triggers action simulation*, while in mental imagery the simulation process is triggered by a deliberate act; one purposely decides to imagine observing something or doing something. An empirical validation of this difference comes from brain imaging experiments carried out on healthy human participants. By comparing the motor centers activated by action observation with those activated during voluntary mental motor imagery, it emerges that only the latter leads to the activation of pre-SMA and of the primary motor cortex (see Ehrsson et al. 2003).

That said, it appears nonetheless that both mental imagery and action observation are kinds of simulation. The main difference is what triggers the simulation process: an internal event, in the case of mental imagery, and an external event, in the case of action observation. This difference leads to slightly different patterns of brain activation. However, both conditions share a common mechanism: the simulation of actions by means of the activation of parietal-premotor cortical networks. I submit that this process of automatic simulation also constitutes a basic level of understanding, a level that does not entail the explicit use of any theory or declarative representation.

The body of emotions

Emotions constitute one of the earliest ways available to the individual to acquire knowledge about its situation, thus enabling her/him to reorganize this knowledge on the basis of the outcome of the relations entertained with others. This points to a strong interaction between emotion and action. We seldom touch, look at, smell, or generally interact with the things and situation that we dislike. We do not "translate" these objects or situations into motor schemas suitable to interact with them, as we normally do with objects and situation triggering positive hedonic reactions. The objects and situations we dislike are rather "translated" into aversive motor schemas, which are "tagged" with negative affective-hedonic connotations. The coordinated activity of sensory-motor and affective neural systems results in the simplification and automatization of the behavioral responses that living organisms are supposed to produce in order to survive. The strict coupling between affect and sensory-motor integration appears to be one of the most powerful drives leading the developing individual to the achievement of progressively more

"distal" and abstract goals (see Gallese and Metzinger 2003; Metzinger and Gallese 2003).

Such a coupling between emotion and action is indeed highlighted by a study of Adolphs et al. (2000), where over 100 brain-damaged patients were reviewed. This study showed that the patients who suffered damage to the sensory-motor cortices were also those who scored worst when asked to rate or name facial emotions displayed by human faces. As underlined by Adolphs (2002, 2003), the integrity of the sensory-motor system appears to be critical for the recognition of emotions displayed by others, 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.

Before addressing the role of embodied simulation in the understanding of emotions, it is necessary to clarify what exactly we refer to when we speak of emotions. There are many different ways to experience an emotion. Emotion is a word that designates and refers to a multidimensional aspect of our life. To experience an emotion can be described as subjectively living "inner body states" of varied intensity and amplitude that can surface, with a variety of degrees of explicitness, as ostensive behaviors, often localized to specific body parts, like the face.

Under both first- and third-person perspectives of emotion experience, a complex state of the organism is accompanied by variable degrees of awareness and meta-awareness, variously indicated as "appraisal". It is common experience to be asked by people we know questions like: "Why are you so angry at me?" without having realized until the very moment in which the question was asked that we were indeed expressing the emotion of anger. We can be in a given emotional state, and express it ostensibly with our body, without fully experiencing its content as the content of a particular emotion. Lambie and Marcel (2002) have distinguished two levels of emotion appraisal; a first-order phenomenal state, what they call "First-order emotion experience", and conscious second-order awareness. Both states can be either self-directed (first-person perspective) or world-directed (third person perspective). The content of the first-order phenomenal state is physical, centered on one's body state. The content of second-order conscious awareness can be either propositional or non propositional.

It should be emphasized that it is indeed possible to witness the expression of a given emotional state displayed by someone else without explicitly relying on the propositional description of that state. It is precisely this unmediated, direct form of emotion understanding that I will be addressing here. More specifically, I will characterize the neural underpinnings of a simulation-based type of basic social emotion understanding.

Recent empirical support for a tight link between embodied simulation and our perception of the emotions of others as displayed by their facial expressions, comes from an fMRI study on healthy participants by Carr et al. (2003).

This study shows that both observation and imitation of the facial expression of emotions activate the same restricted group of brain structures, including the ventral premotor cortex, the insula and the amygdala. These data show that the perception and production of emotion-related facial expressions, both impinge upon common neural structures whose function could be characterized as that of a neural mirror matching mechanism. However, one might argue that pretence, the purposive enactment of the overt body expression of an emotion, doesn't grant its characteristic phenomenal awareness. Imitating the expression of emotions doesn't necessarily produce the first-person experience of the emotion one is imitating.

In a recently published fMRI study carried out on healthy human participants, we specifically addressed the issue whether the first- and third-person experience of a particular emotion are mapped by a shared neural representation. To that purpose, we scanned the brain activity of healthy participants during the phenomenal experience of disgust, by having them inhaling disgusting odorants, and during the observation of the same emotion as displayed by video clips of other individuals dynamically expressing it with their facial expression. The results of this study showed that witnessing the facial expression of disgust of others activates the left anterior insula at the same overlapping location activated by the first-person subjective experience of disgust (Wicker et al. 2003). The anterior sector of the insula receives rich connections from olfactory and gustatory structures and from the anterior sectors of the ventral bank of the superior temporal sulcus, where cells have been found in the monkey to respond to the sight of faces (Bruce et al. 1981; Perrett et al. 1982). The anterior insula thus appears to link gustatory, olfactory and visual stimuli with visceral sensations and the related autonomic and viscero-motor responses. Penfield and Faulk (1955) electrically stimulated the anterior insula in humans undergoing neurosurgery. During the stimulation the patients reported feeling nauseous and sick. Krolak-Salmon et al. (2003), by using shorter and weaker stimulation parameters evoked unpleasant sensations in the throat and mouth. These results support the link between the anterior viscero-motor insula and the experience of disgust or related aversive visceral sensations and viscero-motor reactions.

A few clinical cases also show that when the anterior insula is damaged, both the subjective experience of disgust and the capacity to recognize this emotion in others are seriously impaired. Calder et al. (2000) report the case of the patient NK, who after lesions of the left insula and neighbouring structures was selectively impaired in recognising disgust in the facial expressions of others. This incapacity to perceive disgust extended to the auditory modality: he did not recognise the emotional valence of sounds typical for disgust such as retching, while easily recognising that of sounds characteristic of other emotions such as laughter. His recognition of the facial expression of other emotions, including that of fear, was normal. What is most interesting for our

discussion is the fact that the multimodal perceptual deficit for disgust of NK was mirrored by an equivalent deficit in NK's first-person experience of the same emotion. He reported having a reduced sensation of disgust, ranking almost two standard deviations below the normal score in a questionnaire measuring the emotional experience of disgust. His experience of other emotions, though, was fairly normal.

A similar pattern of deficits was reported by Adolphs et al. (2003). They described the patient B who, following bilateral damage to the insula, showed substantial deficits in recognizing the facial expression of disgust, while preserving his recognition of other facial expressions. Patient B's incapacity to experience disgust is evident from the fact that he ingests food indiscriminately, including inedible items, and fails to feel disgust when presented with stimuli representing disgusting food items.

Experiencing disgust and witnessing the same emotion expressed by the facial mimicry of someone else both activate the same neural structure, the anterior insula. The damage of this structure impairs both the capacity to experience disgust and that of recognizing it in others. This suggests, at least for the emotion of disgust, that the first- and third-person experience of a given emotion is underpinned by the activity of a shared neural substrate. When I see a given facial expression, and this perception leads me to understand that expression as characterized by a particular affective state, I do not accomplish this type of understanding through an argument by analogy. The other's emotion is constituted and understood by means of an embodied simulation producing a shared body state. It is the body state shared by the observer and the observed that enables direct understanding. A similar simulation-based mechanism has been proposed by Goldman and Sripada (2005) as "unmediated resonance".

Of course, embodied simulation is not the only functional mechanism underpinning emotion understanding. Emotional stimuli can also be understood on the basis of the explicit cognitive elaboration of their visual aspects. These two mechanisms are not mutually exclusive. Embodied simulation, probably the most ancient mechanism from an evolutionary point of view, is experience-based, while the second mechanism is a cognitive description of an external state of affairs.

Being "in touch"

In the posthumously published second book of his *Ideas* (1989), Husserl points out that the lived body (*Leib*) is the constitutive foundation of any perception, the perception of others included. Were we adopting this perspective to frame social cognition, we could say that the self-modeling functional architecture of the alive body scaffolds the modeling of the intentional relations of other individuals. The multimodal dynamic model of our body as of a goal-seeking

organism, brings about the basic representational architecture for the mapping of intentional relations. The empirical evidence so far reviewed on action and emotion perception seems to support this line of thought. Let us focus now on tactile sensations as the target of our social perception.

Touch has a privileged status in making possible the social attribution of alive personhood to others. "Let's be in touch" is a common expression in everyday language, which metaphorically describes the wish to keep on being related, being in contact with someone else. Such examples show how the tactile dimension is intimately related to the interpersonal dimension. New empirical evidence suggests that the first-person subjective 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, likely exceeding the limits of the traditional unimodal second somatosensory area, there is a localized neural network similarly activated by the self-experienced sensation of being touched, and the perception of an external tactile relation.

Such an activation, obtained during the perception of another body being touched, could perhaps be more parsimoniously interpreted as the outcome of the prediction of a body impact on the observer's own body. However, in sharp contrast with what this interpretation would have predicted, the manipulation of the perspective (subjective vs. objective) under which the observed tactile stimulation was presented to participants did not modify the degree of activation of the same overlapping region within SII-PV. Thus, visual stimuli activate SII/PV in a way that is unaffected by how easily they can be integrated into our body schema.

In a second experiment, we replaced the legs of the actors in the video clips by inanimate objects: rolls of paper towels and binders. Results indicated that even seeing an object getting touched produced a significantly larger activation of SII/PV compared to seeing the object being only approached (see Keysers et al. 2004). The touching of two surfaces in the outside world is something in principle very abstract, if only visually mapped. Mapping it onto what we feel when one of the surfaces being touched is our own body, fills this abstract visual event with a very personal meaning: what it feels like to be touched. It appears therefore that the critical stimulus for SII/PV activation is the perception of touch; be it the touch of an object, another human being, or our own legs. This double pattern of activation of the same brain region seems to suggest that both our capacity to recognize and implicitly understand the tactile experience of others, and a more abstract notion of touch (as in the case of object touch) could be mediated by embodied simulation.

These results suggest that the full appreciation of others as persons like us depends upon the involvement of body-related first-person tactile experiential knowledge. Again, this perspective is closely related to Husserl's notion of intersubjectivity. As repeatedly stated in *Ideas II* (1989), the dual nature of

our own body as the *sensing subject* and the *sensed object* of our perceptions, enables the constitution of other living humans as understandable persons. The body simultaneously perceived as an external object and as an experiential subject grounds within the same substrate made of flesh the sense of experiential personhood we attribute to others. We retrieve the inner sense of the experiences and motivations of others from the their overt behavior because it induces the activation of the same functional mechanisms enabling our own sense of personhood.

The many sides of simulation

The notion of simulation is employed in many different domains, often with different, not necessarily overlapping meanings. Simulation is a functional process that possesses a certain representational content, typically focusing on possible states of its target object. For example, an authoritative view on motor control characterizes simulation as the mechanism employed by forward models to predict the sensory consequences of impending actions. According to this view, the predicted consequences are the simulated ones.

In philosophy of mind, on the other hand, the notion of simulation has been used by the proponents of Simulation Theory of mindreading to characterize the pretend state adopted by the attributer in order to understand others' behavior (see Gordon 1986, 1995, 2000, 2005; Goldman 1989, 1992a,b, 1993a,b, 2000).

I employed the term simulation as an automatic,[1] unconscious, and prereflexive functional mechanism, whose function is the modeling 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 behavior of others, but rather a basic functional mechanism of our brain. However, because it also generates representational content, this functional mechanism seems to play a major role in our epistemic approach to the world. It represents the outcome of a possible action, emotion, or sensation 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.

Successful perception requires the capacity of predicting upcoming sensory events. Similarly, successful action requires the capacity of predicting the expected consequences of action. As suggested by an impressive and coherent amount of neuroscientific data (for a review, see Gallese 2003a), both types of predictions seem to depend on the results of unconscious and automatically driven neural states, functionally describable as simulation processes.

According to the use made of this notion in the present paper, simulation is not conceived of as being confined to the domain of motor control, but rather as a more general and basic endowment of our brain. It is mental because

it has content, but it is sensory-motor because its function is realized by the sensory-motor system. I call it "embodied" – not only because it is neurally realized, but also because it uses a pre-existing body-model in the brain, and therefore involves a non-propositional form of self-representation.

In this context, action simulation in social cognition can also be seen as an exaptation. It is possible that there has never been any "special design" for the function I describe here. It might be an extended functionality later co-opted from a distinct original adaptational functionality, namely, sensory-motor integration for body control purposes.

Conclusions

The main points of the present paper are the following. First, the same neural structures modeling the functions of our body in the world also contribute to our awareness of our lived body in the world and of the objects that the world contains. Embodied simulation constitutes the functional mechanism at the basis of this dual property of the same neural circuits. If this is true, the posited sharp dichotomy between neural correlates of body schema and body image should be questioned. Most importantly, the rigid distinction between an unconscious system responsible for controlling our body in the world and the conscious awareness of the properties that the same body instantiates should also be questioned. It is worth noting that the somatosensory system is not only responsible for the somatotopic mapping of incoming sensory stimuli, but is also crucial in producing the body's self-awareness, by means of the peculiar experience of double-touch. As Husserl (1989) points out, "... I do not see my body, the way I touch myself: What I call the seen Body is not something seeing which is seen, the way my body as touched is something touching which is touched" (Ideas II, p. 155).

Second, there are neural mechanisms mediating between the multi level personal background experience we entertain of our lived body, and the *implicit certainties* we simultaneously hold about others. Such personal body-related experience enables us to understand the actions performed by others, and to directly decode the emotions and sensations they experience. Our seemingly effortless capacity to conceive of the acting bodies inhabiting our social world as *goal-oriented persons* like us depends on the constitution of a shared meaningful interpersonal space. This shared manifold space can be characterized at the functional level as embodied simulation, a specific mechanism, likely constituting a basic functional feature by means of which our brain/body system models its inter-actions with the world. Embodied simulation constitutes a crucial functional mechanism in social cognition, and it can be neurobiologically characterized. The mirror neurons matching systems represent the sub-personal instantiation of this mechanism (see also Gallese et al. 2005).

The neuroscientific evidence reviewed here suggests that social cognition is tractable at the neural level of description. This level is implicit, though, when the organism is confronting the intentional behavior of others, it produces a specific phenomenal state of "intentional attunement". This phenomenal state generates a peculiar quality of familiarity with other individuals, produced by the collapse of the others' intentions into the observer's ones. This of course doesn't account for all of our mentalizing abilities. Our most sophisticated mentalizing abilities likely require the activation of large regions of our brain, certainly larger than a putative domain-specific Theory of Mind Module. For example, the same actions performed by others in different contexts can lead the observer to radically different interpretations. Thus, social stimuli can also be understood on the basis of the explicit cognitive elaboration of their contextual aspects and of previous information. These two mechanisms are not mutually exclusive. Embodied simulation is experience-based, while the second mechanism is a cognitive description of an external state of affairs. I posit that embodied simulation scaffolds the propositional, more cognitively sophisticated mentalizing mechanism. When the former mechanism is not present or malfunctioning, as in autism, the latter can provide only a pale, detached account of the social experiences of others (Gallese 2004).

The sharp distinction, classically drawn between the first- and third-person experience of actions, emotions, and sensations, appears to be much more blurred at the level of the sub-personal mechanisms mapping it. The gap between the two perspectives is bridged by the way the intentional relation is functionally mapped at the neural-body level. Any intentional relation can be mapped as a relation holding between a subject and an object. The mirror neural circuits described in the second part of the paper map the different intentional relations in a compressed and indeterminate fashion, which is neutral about the specific quality or identity of the agentive/subjective parameter. By means of a shared functional state realized in two different bodies that nevertheless obey the same functional rules, the "objectual other" becomes "another self".

The shareability of the phenomenal content of intentional relations as mediated by sensory-motor multimodally integrated neural circuits, has interesting consequences – both from a theoretical and empirical point of view – for the debate on how semantics is mapped in the brain. The picture conveyed by the neuroscientific data I reviewed here suggests the necessity to cut across the widely endorsed dichotomy between distinct semantic and pragmatic cognitive domains. Social meaning is primarily the object of practical concern, and not of theoretical judgement (see Millikan 2004). It relies on non-inferential mechanisms, which do not require the explicit use of rationality. As put by Gordon (2005), the implicit recognition of conspecifics as intentional agents like oneself is a case of procedural rather than declarative knowledge.

Furthermore, if embodied simulation and its neural counterpart – the mirror neurons circuits – do indeed constitute a non-propositional mechanism for social meaning attribution, the sharp dichotomy between a semantic/pragmatic division of labour among brain areas (see Goodale and Milner 1992; Jacob and Jeannerod 2003), should also be questioned.

The ideas discussed in this paper are aimed to provide building blocks for a general neuroscientific account of basic aspects of phenomenal experience. Future neuroscientific research will hopefully provide further empirical tests to their validity.

Acknowledgments

Note

1. It is "automatic" in the sense that it is obligatory.

References

Adolphs, R. 2002. Neural systems for recognizing emotion. *Curr. Opin. Neurobiol.* 12(2): 169–177.

Adolphs, R. 2003. Cognitive neuroscience of human social behaviour. *Nat. Rev. Neurosci.* 4(3): 165–178.

Adolphs, R., Tranel, D. and Damasio, A. R. 2003. Dissociable neural systems for recognizing emotions. *Brain Cogn.* 52(1): 61–69.

Adolphs, R., Damasio, H., Tranel, D., Cooper, G. and Damasio, A. R. 2000. A role for somatosensory cortices in the visual recognition of emotion as revealed by three-dimensional lesion mapping. *J. Neurosci.* 20: 2683–2690.

Berti, A. and Frassinetti, F. 2000. When far becomes near: Re-mapping of space by tool use. *Journal of Cognitive Neuroscience* 12: 415–420.

Berti, A. and Rizzolatti, G. 1992. Visual processing without awareness: Evidence from unilateral neglect. *Journal of Cognitive Neuroscience* 4: 345–351.

Bruce, C., Desimone, R. and Gross, C. G. 1981. Visual properties of neurons in a polysensory area in superior temporal sulcus of the macaque. *J. Neurophysiol.* 46: 369–84.

Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R. J., Zilles, K., Rizzolatti, G. and Freund, H.-J. 2001. Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. *European Journal of Neuroscience* 13: 400–404.

Buccino, G., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., Porro, C. A. and Rizzolatti, G. 2004. Neural circuits involved in the recognition of actions performed by nonconspecifics: An fMRI study. *J. Cogn. Neurosci.* 16: 114–126.

Calder, A. J., Keane, J., Manes, F., Antoun, N. and Young, A. W. 2000. Impaired recognition and experience of disgust following brain injury. *Nat. Neurosci.* 3: 1077–1078.

Carr, L., Iacoboni, M., Dubeau, M. C., Mazziotta, J. C. and Lenzi, G. L. 2003. Neural mechanisms of empathy in humans: A relay from neural systems for imitation to limbic areas. *Proc. Natl. Acad. Sci. USA* 100(9): 5497–5502.

Cochin, S., Barthelemy, C., Lejeune, B., Roux, S. and Martineau, J. 1998. Perception of motion and qEEG activity in human adults. *Electroenc. Clin. Neurophysiol.* 107: 287–295.

Cowey, A., Small, M. and Ellis, S. 1994. Left visuo-spatial neglect can be worse in far than near space. *Neuropsychologia* 32: 1059–1066.

Cowey, A., Small, M. and Ellis, S. 1999. No abrupt change in visual hemineglect from near to far space. *Neuropsychologia* 37: 1–6.

Decety, J. and Grèzes, J. 1999. Neural mechanisms subserving the perception of human actions. *Trends in Cognitive Sciences* 3: 172–178.

Decety, J., Grezes, J., Costes, N., Perani, D., Jeannerod, M., Procyk, E., Grassi, F. and Fazio, F. 1997. Brain activity during observation of actions. Influence of action content and subject's strategy. *Brain* 120: 1763–1777.

Duhamel, J-R., Bremmer, F., Ben Hamed, S. and Graf, W. 1997. Spatial invariance of visual receptive fields in parietal cortex neurons. *Nature* 389: 845–848.

Ehrsson, H. H., Geyer, S. and Naito, E. 2003. Imagery of voluntary movement of fingers, toes, and tongue activates corresponding body-part-specific motor representations. *J. Neurophysiol.* 90(5): 3304–3316.

Fadiga, L., Fogassi, L., Pavesi, G. and Rizzolatti, G. 1995. Motor facilitation during action observation: A magnetic stimulation study. *J. Neurophysiol.* 73: 2608–2611.

Ferrari, P. F., Gallese, V., Rizzolatti, G. and Fogassi, L. 2003. Mirror neurons responding to the observation of ingestive and communicative mouth actions in the monkey ventral premotor cortex. *European Journal of Neuroscience* 17: 1703–1714.

Fogassi, L., Gallese, V., Fadiga, L. and Rizzolatti, G. 1996a. Space coding in inferior premotor cortex (area F4): Facts and speculations. In: F. Laquaniti and P. Viviani (eds.), *Neural Basis of Motor Behavior* (pp. 99–120). NATO ASI Series, Dordrecht: Kluwer Academic Publishers.

Fogassi, L., Gallese, V., Fadiga, L., Luppino, G., Matelli, M. and Rizzolatti, G. 1996b. Coding of peripersonal space in inferior premotor cortex (area F4). *J. Neurophysiol.* 76: 141–157.

Gallese, V. 2000. The acting subject: Towards the neural basis of social cognition. In: T. Metzinger (ed.), *Neural Correlates of Consciousness. Empirical and Conceptual Questions* (pp. 325–333). Cambridge, MA, MIT Press.

Gallese, V. 2001. The "Shared Manifold" Hypothesis: From mirror neurons to empathy. *Journal of Consciousness Studies* 8(5–7): 33–50.

Gallese, V. 2003a. The manifold nature of interpersonal relations: The quest for a common mechanism. *Phil. Trans. Royal Soc. London B.* 358: 517–528.

Gallese, V. 2003b. The roots of empathy: the shared manifold hypothesis and the neural basis of intersubjectivity. *Psychopathology* 36(4): 171–180.

Gallese, V. 2003c. A neuroscientific grasp of concepts: From control to representation. *Phil. Trans. Royal Soc. London, B.* 358: 1231–1240.

Gallese, V. 2005. "Being like me": Self-other identity, mirror neurons and empathy. In :S. Hurley and N. Chater (eds.), *Perspectives on Imitation: From Cognitive Neuroscience to Social Science* (Vol. 1). Cambridge, MA: MIT Press.

Gallese, V. 2004. Intentional attunement. The mirror neuron system and its role in interpersonal relations. http://www.interdisciplines.org/mirror/papers/1

Gallese, V. and Goldman, A. 1998. Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Sciences* 12: 493–501.

Gallese, V. and Lakoff, G. 2005. The brain's concepts: The role of the sensory-motor system in conceptual knowledge. *Cogn. Neuropsychol* (in press).

Gallese, V. and Metzinger, T. 2003. Motor ontology: The representational reality of goals, actions, and selves. *Philosophical Psychology* 13(3): 365–388.

Gallese, V., Fadiga, L., Fogassi, L. and Rizzolatti, G. 1996. Action recognition in the premotor cortex. *Brain* 119: 593–609.

Gallese, V., Keysers, C. and Rizzolatti, G. 2004. A unifying view of the basis of social cognition. *Trends in Cognitive Sciences* 8: 396–403.

Gallese, V., Fogassi, L., Fadiga, L. and Rizzolatti, G. 2002b. Action Representation and the inferior parietal lobule. In: W. Prinz and B. Hommel (eds.), *Attention and Performance* XIX (pp. 247–266). Oxford: Oxford University Press.

Gentilucci, M., Scandolara, C., Pigarev, I. N. and Rizzolatti, G. 1983. Visual responses in the postarcuate cortex (area 6) of the monkey that are independent of eye position. *Experimental Brain Research* 50: 464–468.

Gentilucci, M., Fogassi, L., Luppino, G., Matelli, M., Camarda, R. and Rizzolatti, G. 1988. Functional organization of inferior area 6 in the macaque monkey: I. Somatotopy and the control of proximal movements. *Experimental Brain Research* 71: 475–490.

Goldman, A. 1989. Interpretation psychologized. *Mind and Language* 4: 161–185.

Goldman, A. 1992a. In defense of the simulation theory. *Mind and Language* 7: 104–119.

Goldman, A. 1992b. Empathy, mind, and morals: Presidential address. *Proceedings and Addresses of the American Philosophical Association* 66: 17–41.

Goldman, A. 1993a. The psychology of folk psychology. *Behavioral Brain Sciences* 16: 15–28.

Goldman, A. 1993b. *Philosophical Applications of Cognitive Science*. Boulder, Colo., Westview Press.

Goldman, A. 2000. The mentalizing folk. In: D. Sperber (ed.), *Metarepresentation*, London, Oxford University Press.

Goldman, A. and Gallese, V. 2000. Reply to Schulkin. *Trends in Cognitive Sciences* 4: 255–256.

Goldman, A. and Sripada, C. S. 2005. Simulationist models of face-based emotion recognition. *Cognition* (in press).

Goodale, M. A. and Milner, A. D. 1992. Separate visual pathways for perception and action. *Trends Neurosci* 15: 20–25.

Gordon, R. 1986. Folk psychology as simulation. *Mind and Language* 1: 158–171.

Gordon, R. 1995. Simulation without introspection or inference from me to you. In: M. Davies and T. Stone (eds.), *Mental Simulation* (pp. 53–67). Oxford: Blackwell.

Gordon, R. 1996. 'Radical' simulationism. In: P. Carruthers and P. Smith (eds.), *Theories of Theories of Mind* (pp. 11–21). Cambridge, UK: Cambridge University Press.

Gordon, R. 2005. Intentional agents like myself. In: S. Hurley and N. Chater (eds.), *Perspectives on Imitation: From Cognitive Neuroscience to Social Science* (Vol. 2). Cambridge, MA: MIT Press, in press.

Grafton, S. T., Arbib, M. A., Fadiga, L. and Rizzolatti, G. 1996. Localization of grasp representations in humans by PET: 2. Observation compared with imagination. *Exp. Brain Res.* 112: 103–111.

Graziano, M. S. A. and Gross, C. G. 1995. The representation of extrapersonal space: A possible role for bimodal visual-tactile neurons. In: M. S. Gazzaniga (ed.), *The Cognitive Neurosciences* (pp. 1021–1034). Cambridge, MA: MIT Press.

Graziano, M. S. A., Hu, X. and Gross, C. G. 1997a. Visuo-spatial properties of ventral premotor cortex. *J. Neurophysiol.* 77: 2268–2292.

Graziano, M. S. A., Hu, X. and Gross, C. G. 1997b. Coding the locations of objects in the dark. *Science* 277: 239–241.

Graziano, M. S. A., Reiss, L. A. J. and Gross, C. G. 1999. A neuronal representation of the location of nearby sounds. *Nature* 397: 428–430.

Graziano, M. S. A., Yap, G. S. and Gross, C. G. 1994. Coding of visual space by premotor neurons. *Science* 266: 1054–1057.

Halligan, P. W. and Marshall, J. C. 1991. Left neglect for near but not far space in man. *Nature* 350: 498–500.

Hari, R., Forss, N., Avikainen, S., Kirveskari, S., Salenius, S. and Rizzolatti, G. 1998. Activation of human primary motor cortex during action observation: A neuromagnetic study. *Proc. Natl. Acad. Sci. USA* 95: 15061–15065.

Husserl, E. 1925/1962. *Phänomenologische Psychologie* (1925) (Husserliana, vol. IX), Martinus Nijhoff, Den Haag.

Husserl, E. 1989. *Ideas Pertaining to a Pure Phenomenology and to a Phenomenological Philosophy Second Book: Studies in the Phenomenology of Constitution*. Dordrecht: Kluwer Academic Publishers.

Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C. and Rizzolatti, G. 1999. Cortical mechanisms of human imitation. *Science* 286: 2526–2528.

Jacob, P. and Jeannerod, M. 2003. *Ways of Seeing – The Scope and Limits of Visual Cognition.* Oxford: Oxford University Press.

Keysers, C., Kohler, E., Umiltà, M. A., Fogassi, L., Rizzolatti, G. and Gallese, V. 2003. Audio-visual mirror neurones and action recognition. *Exp. Brain Res.* 153: 628–636.

Keysers, C., Wickers, B., Gazzola, V., Anton, J.-L., Fogassi, L. and Gallese, V. 2004. A touching sight: SII/PV activation during the observation and experience of touch. *Neuron* 42(22): 1–20.

Kohler, E., Keysers, C., Umiltà, M. A., Fogassi, L., Gallese, V. and Rizzolatti, G. 2002. Hearing sounds, understanding actions: Action representation in mirror neurons. *Science* 297: 846–848.

Krolak-Salmon, P., Henaff, M. A., Isnard, J., Tallon-Baudry, C., Guenot, M., Vighetto, A., Bertrand, O. and Mauguiere, F. 2003. An attention modulated response to disgust in human ventral anterior insula. *Ann. Neurol.* 53: 446–453.

Lambie, J. A. and Marcel, A. J. 2002. Consciousness and the varieties of emotion experience: A theoretical framework. *Psychol. Rev.* 109: 219–259.

Marshall, J. F. and Halligan, P. W. 1988. Blindsight and insight in visuo-spatial neglect. *Nature* 336: 766–767.

Metzinger, T. and Gallese, V. 2003. The emergence of a shared action ontology: Building blocks for a theory. *Consciousness and Cognition* 12: 549–571.

Penfield, W. and Faulk, M. E. 1955. The insula: Further observations on its function. *Brain* 78: 445–70.

Millikan, R. G. 2004. *Varieties of Meaning*. Boston, MA: MIT Press, in press.

Perrett, D. I., Rolls, E. T. and Caan, W. 1982. Visual neurones responsive to faces in the monkey temporal cortex. *Exp. Brain Res.* 47: 329–342.

Rizzolatti, G., Berti, A. and Gallese, V. 2000. Spatial neglect: Neurophysiological bases, cortical circuits and theories. In: F. Boller, J. Grafman, and G. Rizzolatti (eds.), *Handbook of Neuropsychology* 2nd Edition (Vol. I), Amsterdam; Elsevier Science B.V., pp. 503–537.

Rizzolatti, G., Matelli, M. and Pavesi, G. 1983. Deficits in attention and movement following the removal of postarcuate (area 6) and prearcuate (area 8) cortex in macaque monkeys. *Brain* 106: 655–673.

Rizzolatti, G., Fogassi, L. and Gallese, V. 2000. Cortical mechanisms subserving object grasping and action recognition: A new view on the cortical motor functions. In: M. S.

Gazzaniga (ed.), *The Cognitive Neurosciences* (pp. 539–552), 2nd edition. Cambridge, MA: MIT Press.

Rizzolatti, G., Fogassi, L. and Gallese, V. 2001. Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Neuroscience Reviews*, 2: 661–670.

Rizzolatti, G., Fogassi, L. and Gallese, V. 2002. Motor and cognitive functions of the ventral premotor cortex. *Curr. Op. Neurobiol*. 12: 149–154.

Rizzolatti, G., Fadiga, L., Gallese, V. and Fogassi, L. 1996a. Premotor cortex and the recognition of motor actions. *Cog. Brain Res*. 3: 131–141.

Rizzolatti, G., Fadiga, L., Matelli, M., Bettinardi, V., Paulesu, E., Perani, D. and Fazio, G. 1996b. Localization of grasp representations in humans by PET: 1. Observation versus execution. *Exp. Brain Res*. 111: 246–252.

Searle, J. 1992. *The Rediscovery of the Mind*. Cambridge, MA: London, England: MIT Press, A Bradford Book.

Umiltà, M. A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C. and Rizzolatti, G. 2001. "I know what you are doing": A neurophysiological study. *Neuron* 32: 91–101.

Zahavi, D. 2002. First-person thoughts and embodied self-awareness: Some reflections on the relation between recent analytical philosophy and phenomenology. *Phenomenology and the Cognitive Sciences* 1: 7–26.

Watkins, K. E., Strafella, A. P. and Paus, T. 2003. Seeing and hearing speech excites the motor system involved in speech production. *Neuropsychologia* 41(8): 989–994.

Wicker, B., Keysers, C., Plailly, J., Royet, J.-P., Gallese, V. and Rizzolatti, G. 2003. Both of us disgusted in my insula: The common neural basis of seeing and feeling disgust. *Neuron* 40: 655–664.