

In press in: Higher-order motor disorders: from Neuroanatomy and Neurobiology to Clinical Neurology. Eds. Freund H.J., Jeannerod M., Hallett M. (New York: Oxford University Press)

The mirror-neuron system and action recognition

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Introduction

Understanding actions made by others is a fundamental cognitive function on which social life and the survival of individuals depend. Despite its crucial role in social behavior, action understanding, unlike other cognitive capacities such as, for example, object or space perception, has never been a central topic in neuroscience. Only recently with the discovery of mirror neurons (Gallese et al. 1996; Rizzolatti et al. 1996a), action understanding and phenomena closely related to this function, such as for example imitation, become object of intense investigation (see for review Rizzolatti et al. 2001)

How do we understand actions made by other individuals? Which are the neurophysiological bases of this capacity? There are various accounts that might explain how action understanding may occur. The most intuitive one, which we will designate as “visual hypothesis”, is that action understanding is based on a visual analysis of the different elements forming an action and on their inter-relations. Let us take, for example, the observation of a girl biting an apple. The action is first decomposed in its elements: the hand, the apple, and the movement of the hand toward the apple. Then the combination of these elements, plus inferences from their semantics, allows the observer to understand the witnessed action. No motor or emotional involvement is required. This mechanism may be present in a living creature as well as in an artifact, for example in a robot that (obviously) has no idea whatsoever of what eating means.

If this view is correct, action understanding should be mediated by the activity of the extrastriate visual areas, the inferotemporal lobe, and the superior temporal sulcus areas. In both monkeys and humans these areas respond selectively to objects, body parts, biological motion, and, in the case of some neurons of STS, to interactions between hands and objects (Gross 1972; Perrett et al. 1989; Tanaka et al. 1991; Ungerleider and Haxby 1994; Carey et al. 1997; Allison et al. 2000; Kanwisher 2000).

A possible different hypothesis is that we understand actions when we map the visual representation of the observed action on the motor representations of the same action. We will designate it as the "direct matching hypothesis". According to this hypothesis, an action is understood when its observation makes to "resonate" the motor system of the observer. Thus, when we observe the girl biting an apple, the same populations of neurons that control the execution of biting will resonate in the observer's motor areas. By means of such a mechanism, the "motor knowledge" of the observer will be used to understand the observed action. The hypothesis that action understanding is based upon a direct matching mechanism doesn't exclude, of course, that other visual and cognitive processes based on object and movement descriptions may also play a role in action recognition. It stresses however, the primacy of direct action observation/execution matching.

The two accounts of action recognition presented above refer to "cold" actions, that is to actions devoid of an emotional content. It is likely that different mechanisms are involved in the understanding of others' actions that induce emotions or have consequence on the welfare of the observer. In these cases again there appear to be two major possibilities. If the action of the others may produce harm, as in the case of attack or more generally in the case of aggressive behavior, the action is understood because its visual description is associated with its consequences. No involvement of the motor system of the observer is necessary. Note that here, unlike in the visual recognition of cold action, is the correlation between a visually event and what is going to occur and not the correlation between various visual events that is at the basis of action recognition.

Finally, also in the case of "hot" actions (those with an emotional content), a resonance mechanism may play a fundamental role in action recognition ("direct matching hypothesis"). In this case, however, the resonating structures are not those coding the cold motor behavior, but those that mediate the visceromotor reactions

expressing emotions. Preliminary evidence shows that structures such as insula are involved in this process (Carr et al. 2003; Keysers et al., in preparation)

The present chapter is structured in the following way. We describe first the mirror-neuron system in the monkey. We provide then evidence that this system is present also in humans. Finally, we argue that the basic function of the mirror-neuron system is action recognition and that at the top of this older capacity, other faculties evolved in humans such as imitation and the faculty of language. Emotional behavior will be not dealt with.

The mirror-neuron system in monkeys

Mirror neurons were first discovered in area F5 of the monkey premotor cortex (Di Pellegrino et al. 1992; Gallese et al. 1996; Rizzolatti et al. 1996a). F5 is basically a motor area that controls hand and mouth movements. A fundamental characteristic of this area is that many of its neurons discharge during specific goal-directed action such as grasping, holding or tearing (Rizzolatti et al. 1988). Many of these neurons become active regardless of the effector (the right hand, the left hand or the mouth) that is used to achieve the goal (e.g. grasping an object). Conversely, they do not fire when the monkey uses the same effectors but for another purpose (e.g. pushing away objects).

A second fundamental characteristic of area F5 is that many of its neurons specify how a goal can be achieved. For example, the majority of grasping neurons discharge only if grasping is made using a particular type of prehension, such as precision grip, finger prehension and, more rarely, whole hand prehension.

About 20% of F5 neurons respond to visual stimuli (Rizzolatti et al. 1988). One class of these visuo-motor neurons, named *canonical neurons*, discharge when the monkey sees an object that is congruent with the type of grip coded by the neuron (Murata et al. 1997). A second class of visuo-motor neurons does not discharge in response to the presentation of 3-D objects. The visual stimuli effective in triggering them are actions in which the experimenter (or a monkey) interacts with objects. Neurons with these properties were called *mirror neurons* (Gallese et al. 1996; Rizzolatti et al. 1996a).

Typically, F5 mirror neurons, in order to be triggered, require an interaction between hand and object. The sight of the object alone or of the agent mimicking an action is ineffective. The object significance for the animal has no influence on mirror neuron response. Grasping a piece of food or a geometric solid produces responses of the same intensity.

An important functional aspect of mirror neurons is the relation between their

visual and motor properties. Virtually all mirror neurons show congruence between the visual actions they respond to and the motor response they code. According to the type of congruence they exhibit, mirror neurons have been subdivided into “strictly congruent” and “broadly congruent” neurons (Gallese et al. 1996).

As “strictly congruent” are defined those mirror neurons in which the effective observed and effective executed actions correspond both in terms of goal (e.g. grasping) and means, that is how the action is executed (e.g. precision grip). They represent about 30% of F5 mirror neurons.

As “broadly congruent” are defined those mirror neurons that, in order to be triggered, do not require the observation of exactly the same action they code motorically. Some of them discharge during the execution of a particular type of action (e.g. grasping) when executed using a particular grip type (e.g. precision grip). However, they respond to the observation of grasping made by another individual, regardless of the type of grip used. Other broadly congruent neurons discharge in association with a single motor action (e.g. holding), but respond to the observation of two actions (e.g. grasping and holding). Broadly congruent neurons are the class of mirror neurons mostly represented (about 60%).

From this short review of basic properties of F5 neurons, it appears that this area is storage of *potential* actions or as we previously described it a “vocabulary of actions” (Rizzolatti et al 1988). The activation of F5 neurons does not determine necessarily an action. It evokes its representation. If other contingencies are met, this potential action becomes a *real* motor action (see Rizzolatti and Luppino 2001). F5 potential actions can be activated endogenously or exogenously. Exogenous (visual) activation is caused by the observation of objects (canonical neurons) or by the observation of actions made by others (mirror neurons).

Another cortical area where there are mirror neurons is area PF (Fogassi et al. 1998; Gallese et al. 2002). This area forms the rostral part of the inferior parietal lobule. PF

receives input from STS, where there are many neurons that become active during the observation of action (Perrett et al. 1989), and sends output to area F5.

Neurons in area PF are functionally heterogeneous. Most of them (about 90%) respond to sensory stimuli (Hyvarinen 1982; Leinonen and Nyman 1979; Fogassi et al. 1998; Gallese et al. 2002). About 50% of them discharge also in association with monkey active movements.

Neurons responding to sensory stimuli have been subdivided into three categories: "somatosensory" neurons (33%), "visual" neurons" (11%) and "bimodal", somatosensory and visual neurons (56%). Among the neurons with visual responses ("visual neurons" and "bimodal neurons"), 41% respond to the observations of actions made by another individual. One third of them, similarly to STS neurons, do not appear to have motor-related activity. The other two-third discharge also during the monkey movement and, in most cases, showed the visuo-motor congruence typical of mirror neurons -"PF mirror neurons" (Gallese et al. 2002).

New evidence for a role of F5 mirror neurons in action understanding

From the very discovery of mirror neurons it was suggested that they play an important role in action understanding. The core of this proposal is the following. When an individual acts he selects an action whose motor consequences are known to him. The mirror neurons allow this knowledge to be extended to actions performed by others. Each time an individual observes an action done by another individual, neurons that represent that action are activated in his or her premotor cortex. Because the evoked motor representation corresponds to that internally generated during active action, the observer understands the witnessed action (see Rizzolatti et al 2001).

This action recognition hypothesis was recently tested by studying mirror neuron responses in conditions in which the monkey was able to understand the meaning of the

occurring action, but without the visual stimuli that typically activate mirror neurons. The rationale of the experiments was the following. If mirror neurons are involved in action understanding, their activity should reflect the action meaning and not specific sensory contingencies.

In a series of experiments the hypothesis was tested by presenting the monkey with auditory stimuli able to evoke the idea of an action (Kholer et al. 2002). F5 mirror neuron activity was recorded while the monkey was observing a “noisy” action (e.g. ripping a piece of paper), or was presented with the same noise without seeing the action producing it. The results (Figure 1) showed that most mirror neurons that discharge to presentation of actions accompanied by sounds discharge also in response to the sound alone (“audiovisual” mirror neurons). The mere observation of the same “noisy” action without sound was also effective. Further experiments showed that a large number of audiovisual mirror neurons respond selectively to specific action sounds. These results strongly support the notion that the discharge of F5 neurons correlates with action understanding and not with the stimuli that determine it. The effective stimuli may be visual or acoustical. Once they specify the action meaning, the neuron fires.

INSERT FIGURE 1 ABOUT HERE

Another series of experiments aimed to test the “direct matching hypothesis” consisted in the study of mirror neurons responses in conditions in which monkey was prevented from seeing the occurring action (and listen to its sound), but were provided with clues on what the action may be. If mirror neurons are involved in action understanding they should discharge also in this condition.

This experiment was recently carried out by Umiltà et al. (2001). The experimental paradigm consisted of two basic conditions. In one, the monkey was shown a fully visible action directed toward an object (“full vision” condition). In the other, the monkey saw the

same action but with its final critical part hidden (“hidden” condition). Before each trial the experimenter placed a piece of food behind the screen so that the monkey knew that there was an object behind it. The main result of the experiment was that more than half of the tested neurons discharged in hidden condition. Out of them, some did not show any difference between hidden and full vision conditions, others responded stronger in full vision.

In conclusion, both the experiments in which the stimulus conditions were altered showed that F5 mirror neuron activation correlates with action representation rather than with the stimulus properties leading to it. This finding strongly supports the notion that F5 activity plays a fundamental role in the understanding of action meaning.

The mirror-neuron system in humans

Evidence that a mirror-neuron system also exists in humans comes from three sources: transcranial magnetic stimulation (TMS) studies, electroencephalographic (EEG) and magnetoencephalographic (MEG) experiments, and brain imaging studies.

TMS studies

The first evidence in favor of the existence of a mirror system in humans came from a study by Fadiga et al. (1995) who stimulated the left motor cortex of normal volunteers. There were in four experimental conditions: a) observation of hand grasping movements; b) of meaningless intransitive arm movements; c) of three-dimensional objects; d) of the dimming of a small spot of light. Movement evoked potentials (MEPs) were recorded from hand muscles.

The rationale of the experiment was the following: if the observation of hand and arm movements made by another individual facilitates the observer’s motor system, this

facilitation should determine an increase of MEPs recorded from hand and arm muscles in comparison to the two control conditions (object observation and the dimming detection task). The results confirmed the hypothesis. A selective increase of motor evoked potentials was found in those muscles of the observer that he/she normally uses for producing them.

The MEPs facilitation during movement observation can be explained in two ways. It may result from an enhancement of primary motor cortex excitability due to excitatory cortical connections reaching the primary motor cortex from the human cortical homologue of monkey of area F5. Alternatively, it may be to a facilitatory output to the spinal cord originating from the mirror human area homologue of F5. Data of an experiment by Strafella and Paus (2000) support the cortico-cortical hypothesis. By using a double-pulse TMS technique they demonstrated that the duration of intracortical recurrent inhibition occurring during action observation is similar to that occurring during action execution.

The same issue was also investigated by Baldissera et al. (2001). These authors examined the modulation of spinal cord excitability during observation of goal directed hand actions by measuring the size of the H-reflex evoked in flexors and extensors muscles in normal human volunteers. They found that, in the absence of any detectable muscle activity, there was a modulation of the reflex amplitude during action observation, specifically related to the different phases of the observed movement. While the H-reflex recorded from flexors rapidly increased in size during hand opening, it was depressed during hand closing and quickly recovered during object lifting. The converse behavior was found in extensors. Thus, while modulation of cortical excitability varies in accordance with the seen movements, the spinal cord excitability changes in the opposite direction.

This result suggests that, at the spinal cord level, there is a mechanism that prevents execution of the seen actions, leaving, thus, free the cortical motor system to “re-act” the

observed actions without the risk of overt movement generation.

Changes of motor cortex excitability during the observation of actions made by others were also reported by Gangitano et al. (2001) and Maeda et al. (2002).

Gangitano et al. (2001) recorded MEPs from the hand muscles of normal volunteers while they were observing grasping movements made by another individual. The MEPs were recorded at different intervals following the movement onset. The results showed that the motor cortical excitability faithfully followed the grasping movement phases of the observed action. This finding indicates that in humans the mirror-neuron system codes for the temporal aspects of the observed movements and not only for the meaning of the observed action.

Maeda et al. (2002) also recorded MEPs from hand muscles of normal volunteers. The recordings were made while the volunteers observed video-clips of different finger movements such as thumb abduction/adduction. The finger movements were presented in two hand orientations: as if the actor was sitting next to the observer (hand “away” position) and as if the actor was in front of the observer (hand “toward” position). The results showed that the degree of cortical motor modulation depended on hand orientation. Modulation was greater when the observed movement was performed in the hand “away” position, (i.e. when the actor and the observer were in the same position) than in the hand “toward” position.

In conclusion, the TMS studies reviewed above show that a mirror-neuron system similar to that found in the monkey is also present in humans. In addition, they demonstrate two important properties of the human mirror-neuron system that do not appear to exist in that of the monkey. First, intransitive meaningless movements produce mirror neuron activation in humans (Fadiga et al. 1995; Maeda et al. 2002), but not in monkeys. Second, the correlation between the time course of the observed movements and the MEPs facilitation suggests that the human mirror-neuron system codes for the movements forming an action, and not only for actions as monkey mirror-neuron system

does. In a previous study (Rizzolatti et al. 1999) we referred to the mirror mechanism describing movements as the “low-level resonance mechanism” contrasting it to the “high-level resonance mechanism” of F5 where the coded element is the action. These properties of the human mirror-neuron system may be an important factor in determining the human capacity for imitation.

EEG and MEG studies.

Evidence in favor of a mirror-neuron system in humans also comes from the study of the reactivity of the cerebral rhythms during movement observation. It is a classical notion that, during motor activity, there is a desynchronization of a specific EEG rhythm (named “mu” rhythm) present in the central cortical derivations. Pioneer experiments by Gastaut and Bert (1954) and Cohen-Seat et al. (1954) showed that action observation also may block the “mu” rhythm.

This finding was recently confirmed by Cochin et al. (1998) who showed desynchronization of central rhythms during the observation of leg movements. Control experiments in which non-biological motions (e.g. a waterfall) were presented to the recorded individuals did not affect the rhythm activity. In a subsequent experiment the same authors compared the cortical electrical activity while participants observed and executed finger movements (Cochin et al. 1999). The results showed that the mu rhythm was blocked in correspondence of the central cortex in both conditions. Similar data were also obtained by Altschuler and colleagues (Altschuler et al. 1997; 2000).

Further evidence for the existence of a mirror-neuron system comes from magnetoencephalography (MEG) studies. These studies showed that, among the various rhythms recorded from the central region, rhythmic oscillations around 20 Hz originate from the precentral cortex inside the central sulcus (Salmelin and Hari 1994; Hari and Salmelin 1997). The level of the 20-Hz activity enhances bilaterally within 500 ms after median nerve stimulation (Salmelin and Hari 1994; Salenius et al. 1997). This after-

stimulation rebound is a highly repeatable and robust phenomenon that can be used as an indicator of the state of the precentral motor cortex. Most interestingly it is abolished when the subject manipulates an object during the median nerve stimulation (Salenius et al. 1997) and is significantly diminished during motor imagery of manipulation movements (Schnitzler et al. 1997).

The post-stimulus rebound method was used to test whether action observation affects the 20 Hz rhythms (Hari et al., 1998). Participants were tested in three conditions: (i) rest, (ii) while they were manipulating a small object, (iii) while they were observing another individual performing the same task. The left and right median nerves were stimulated alternatively and the post-stimulus rebound (15-25 Hz activity) quantified. The results showed that the post-stimulus rebound was strongly suppressed bilaterally during object manipulation and, most interestingly, that it was significantly reduced during action observation. Because the recorded 15-25 Hz activity is known to originate mainly in the precentral motor cortex, these data indicate that human motor cortex is activated both during execution of a motor task and during action observation, a finding strongly supporting the existence of an action observation/execution system in humans.

Brain-imaging studies

The neurophysiological experiments described above, while fundamental in showing that action observation elicits an activation of motor system, do not allow one to localize the areas where mirror-neuron system is localized. Data on this issue have been obtained using brain-imaging techniques.

Early brain imaging studies showed that the observation of hand actions activates (besides various occipital visual areas) the STS region, the inferior parietal lobule, and the ventral premotor cortex plus Broca's area (Rizzolatti et al. 1996b; Grafton et al. 1996; Grèzes et al. 1998; Iacoboni et al. 1999). As previously mentioned, in the monkey neurons discharging during the observation of biological actions are present in the STS region and

in the inferior parietal lobule. Furthermore, mirror neurons are present in the inferior parietal lobule and in the F5 sector of the ventral premotor cortex (PMv). Thus human and monkey cortical circuits active during action observation closely correspond.

A finding that raised some discussion was the activation of Broca's area during the observation of hand action. Although comparative cytoarchitectonic studies indicate that the *pars opercularis* of Broca's area (basically corresponding to area 44) is the human homologue of area F5 (see Petrides and Pandya 1997), the traditional view is that area 44 is the speech motor area. In recent years, however, rich evidence has been accumulating that human area 44, in addition to speech representation, contains (as monkey area F5 does) a hand motor representation (Krams et al. 1998; Binkofski et al. 1999; Iacoboni et al. 1999; Gerardin et al. 2000; Ehrsson et al. 2000; Schubotz and Von Cramon 2001).

The deep-rooted idea that human area 44 is a speech area gave rise to speculations on the possibility that its activation in humans were due to verbal mediation, rather than to motor resonance due to mirror neurons (Grèzes and Decety 2001). New experiments on the general organization of the mirror-neuron system showed that this interpretation of the findings is incorrect.

Buccino et al. (2001) extended the study of the organization of the mirror-neuron system from hand actions to actions made with other effectors. Video-clips showing transitive actions (actions directed toward an object) and intransitive actions made by mouth, hand and foot were used. Action observation was contrasted with the observation of a static face, hand and foot, respectively.

Observation of object-related mouth movements determined activation of the ventral premotor cortex and of the *pars opercularis* of the inferior frontal gyrus (IFG), bilaterally. In addition, two activation foci were found in the parietal lobe. One was located in the rostral part of the inferior parietal lobule (most likely area PF), while the other was located in the posterior part of the same lobule. The observation of intransitive actions determined activation of the same premotor areas, but there was no parietal lobe

activation.

Observation of object-related hand/arm movements determined two areas of activation in the frontal lobe, one corresponding to the *pars opercularis* of IFG, and the other in the upper part of the precentral gyrus. The latter activation was more dorsally located than that found during the observation of mouth movements. Considering the motor organization of PMv, it is likely that the activation of *pars opercularis* was determined by observation of grasping hand movements, while that of dorsal PMv by observation of reaching. As for mouth movements, there were two activation foci in the parietal lobe. The rostral focus was, as in the case of mouth actions, in the rostral part of the inferior parietal lobule, but more posteriorly located, while the caudal focus was essentially in the same location as that for mouth actions. During the observation of intransitive movements the premotor activations were present, but not the parietal ones.

Finally, the observation of object-related foot actions determined an activation of a dorsal sector of the precentral gyrus and an activation of the posterior parietal lobe, in part overlapping with those seen during mouth and hand actions, in part extending more dorsally. Intransitive foot actions produced premotor, but not parietal activation.

The results of this study are important for several reasons. First, they demonstrate that the mirror-neuron system includes a large part of the premotor cortex and the rostral sector of the inferior parietal lobule. Second, they show that the activation map obtained during observation of actions made with different effectors is similar to the motor map obtained with electrical stimulation of the same region (Penfield and Rasmussen 1950; Woolsey, 1958). Finally, they allow one to rule out the idea that the activation of area 44 is due to internal verbalization. Verbalization cannot be present during the observation of hand movements and disappear during the observation of foot movements.

Human beings recognize not only actions done by other human beings, but also actions by individuals belonging to other species. When we observe a monkey or a dog biting a piece of food, we have no difficulty in understanding what the observed animal is

doing. How is this accomplished? Is the understanding of actions done by animals based on the mirror-neuron system? Or is there another mechanism that mediates action recognition in this case?

Recently, an fMRI experiment was carried out in order to answer these questions. Video-clips showing mouth actions performed by humans, monkeys and dogs were presented to normal individuals. Two types of actions were presented: biting and oral communicative actions (speech reading, lip-smacking, barking). As a control, static images of the same actions were presented.

The results (Figure 2) showed that the observation of biting, regardless of whether performed by a man, a monkey or a dog, determined two activation foci in the inferior parietal lobule and activation in the *pars opercularis* of the IFG and the adjacent ventral premotor cortex. The left rostral parietal focus (located in the same position as in the experiments by Buccino et al. just described) and the left premotor focus were virtually identical similar for all three species, while the right side foci were stronger during the observation of actions made by a human being than by an individual of another species.

Observation of speech reading activated the left *pars opercularis* of IFG. Observation of lip smacking, a monkey communicative gesture, activated a small focus in the right and left *pars opercularis* of IFG. Finally, observation of barking did not produce any activation in the frontal lobe.

INSERT FIGURE 2 ABOUT HERE

These results suggest that actions made by other individuals may be recognized through two different mechanisms. Actions belonging to the motor repertoire of the observer are mapped on his/her motor system. Actions that do not belong to this repertoire do not excite the motor system of the observer and appear to be recognized essentially on visual basis.

Mirror-neuron system: Action understanding and imitation

At first glance imitation seems to be a very simple concept: You see something and you do it. However, as soon as the instances in which the term imitation is used are examined, imitation loses its simplicity and appears to include different behaviors, some of them innate, other learned (see Byrne 1995; Tomasello and Call, 1997; Meltzoff and Prinz, 2002).

Imitation strictly defined describes the capacity that individuals of some species (humans in particular) have to learn to do an action from seeing it. This definition, which goes back to Thorndyke (1898), includes two fundamental concepts. Imitation implies *learning*. Imitation implies a *transformation* of an action visually coded into an almost identical action done by the observer. Imitation requires, therefore, a “translation” from sensory to motor domain.

On the top of this there is another fundamental problem. Why does imitation occur? Why an individual wants to repeat an action made by another individual? It is obvious that this desire stems from the belief that doing the observed action will provide benefits.

Thus, imitation of actions made by others requires: a) the comprehension of the goal of the observed action; b) a mechanism translating the observed action from visual to motor domain; c) a learning mechanism that modifies internal motor programs matching them to the observed ones. The properties of mirror neuron meet these requirements.

As already discussed there is convincing evidence showing that the mirror-neuron system is involved in action understanding in both *humans and monkeys*. As far as imitation is concerned, the majority of ethologists agree that this faculty is absent in monkeys (see Byrne 1995; Galef 1988; Whiten and Ham 1992). This indicates that monkeys, although endowed of a mechanism for generating internal copies of actions made by others, are

unable to use them for replicating the observed actions. This capacity developed only later in evolution.

Do humans use the mirror-neuron system for imitation? Evidence accumulating from fMRI and MEG experiments strongly suggests that is the case.

In an fMRI study Iacoboni et al. (1999) instructed normal human volunteers to observe and imitate a finger movement (imitation task) and, in other trials, to perform the same movement in response to a spatial or a symbolic cue (observation/execution tasks). In another series of trials, the same participants were asked to observe identical stimuli, but without responding to them (observation tasks). The results showed that during imitation activation was significantly stronger than in the two non-imitative observation/execution tasks in three cortical areas: *pars opercularis* of the left inferior frontal cortex, the right anterior parietal region, and right parietal operculum. The first two areas were active also during observation tasks, while the parietal operculum was active during observation/execution conditions only.

Remarkably similar results were obtained by Nishitani and Hari (2000) by using the event-related neuromagnetic technique. In their experiment, Nishitani and Hari asked normal human volunteers to grasp a manipulandum, or to observe the same movement performed by an experimenter, or to observe and replicate the observed action on-line. The results showed that during active grasping condition, there was an early activation in the *pars opercularis* of the inferior frontal cortex with a response peak appearing approximately 250 ms before the touch of the target. This activation was followed within 100-200 ms by activation of the left precentral motor area and 150-250 ms later by activation of the right one. During imitation, pattern and sequence of frontal activations were similar to those found during execution, but area 44 activation was preceded by an occipital activation due to visual stimulation present in the imitation condition.

It should be stressed that in the experiments described above as well as in others on neural basis of imitation (Tanaka and Inui 2002; Decety et al. 2002; Koski et al. 2003), the

studied “imitation” was a special case of action execution in which action was elicited by the observation of an identical movement. Imitation, however, according to its classical definition (see above) includes learning. Imitation in this stricter sense has not yet been studied. Preliminary data from an event-related fMRI confirm the central role of the parieto-frontal mirror circuits. They also show, however, contributions of prefrontal, and anterior mesial cortical areas (Buccino et al., in preparation).

Mirror-neuron system: the faculty of language

It has been proposed that mirror-neuron system represents the neurophysiological mechanism from which language evolved (Rizzolatti and Arbib 1998). This proposal is based on the consideration that the mirror-neuron system creates a link between the sender of a message and its receiver. The action made by one individual determines the activation of a similar motor representation in the observer and allows him to understand the meaning of the observed action.

Although, not only in monkeys but (most likely) in our ancestor as well, the primary function of the mirror-neuron system was that of action understanding, this system had intrinsically the potentiality to become the system for voluntarily communication. An important step toward the voluntary use of the mirror-neuron system was the development of a motor “resonance” to intransitive (not object directed) actions, among which pointing to different directions and mimed actions (see Fadiga et al. 1995, Maeda et al. 2002, Buccino et al. 2001). This type of resonance present in humans but not in monkeys, most likely started to appear in primates pertaining to the evolutionary line leading to *homo sapiens*. Its appearance allowed the individuals to describe gesturally space positions, actions and objects. It is worth noting that the semantics of these gestures is not arbitrarily imposed and does not result from an improbable agreement among different

individuals, being intrinsically present in the mirror system.

This evolutionary proposal stresses the importance of gestures in the evolution of language. However, the human language is typically based on the transmission of information via sounds. Recent experiments showed that, in the monkey, a set of mirror neurons, in addition to their visual response, show also a response to the sound of those actions that when observed or executed trigger a given neuron (Kholer et al. 2002). Although these audio-visual mirror neurons do not represent a step toward the development of spoken language, they show that, already in the monkey, there is an auditory access to action representation. Furthermore, they indicate that, before the faculty of language appeared, primates were pre-adapted to associate sounds to actions and understand meaning from sound.

It is impossible at the present to state how the sounds of words became attached to gestures and acquired meaning. We are inclined, however, to think that during the initial phases of speech evolution the sounds accompanying actions were used as a common ground to evoke the meaning of a given action in the listener. Speculations in this sense have been done in the thirties in particular by Paget (1935, cited by Critchley 1939) who claimed that more than 70% of the English words could be explained using this hypothesis.

Regardless of how words acquired meaning, a fundamental step towards speech evolution was the development of a mirror-neurons system for sound imitation. The presence of this system was recently demonstrated in humans by a TMS study in which normal individuals were presented with words that in order to be generated require tongue movements (e.g. "r"). The mere listening to these stimuli produced a strong increase of MEPs recorded from the listener's tongue muscles, as contrasted with word-stimuli that do not require tongue movements or to non-linguistic sounds (Fadiga et al. 2002). This mirror phenomenon for linguistic material appears to be the equivalent of imitation of meaningless arm action in the gesture domain. This phenomenon is very

similar to that originally proposed by Liberman (see Liberman and Whalen, 2000). Note, however, that the existence of this auditory motor resonance does not necessarily imply its involvement in speech perception.

In conclusion, the discovery of mirror-neuron system in primates and of its properties in humans allows one to make some neurophysiological hypotheses on the evolution of the faculty of language in the broad sense (sensory-motor and conceptual-intentional systems). The issue of an evolutionary link between the language faculty in the narrow sense (computational mechanism for recursion) and motor mechanism remains an open question (see Hauser et al. 2002).

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Acknowledgements

This work has been supported by EC grants and by Italian Ministry of University grants to G.R. and to L.F.

Figures

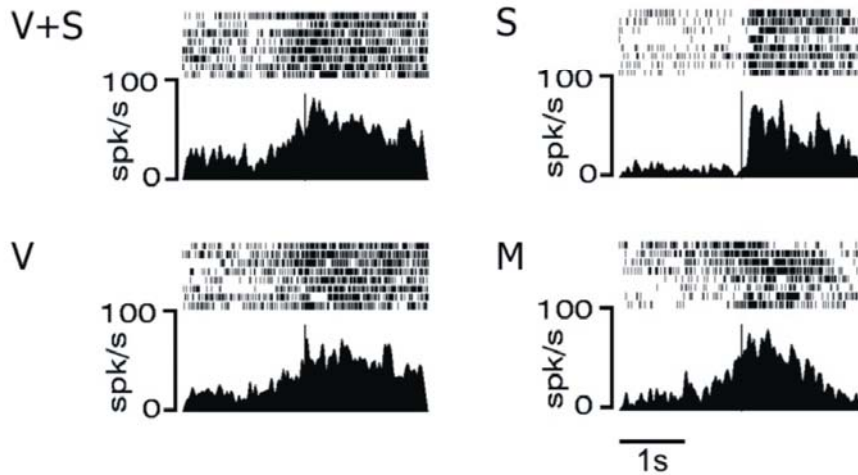


Figure1. Rizzolatti and Fadiga

Figure 1. Example of a mirror neuron selectively responding to action-related sounds. The neuron became active when the monkey observed a peanut breaking action. Sound present (V+S). A similar response was present during the observation of the same action without sound (V) and during sound listening without vision (S). The panel M shows the motor discharge of the same neuron during active grasping. Vertical lines across histograms indicate the time when the sound occurred (V+S, S). In the vision-only condition (V) the stimulus (peanuts) was modified and its breaking did not produce any sound. The vertical line indicates the time when the sound would have occurred in natural condition. In the motor condition (M) the vertical lines indicates the moment when the monkey touched the object. Rasters above each histogram show the neuron's discharge during eight successive trials. Ordinates: spikes/second; Abscissae: seconds.

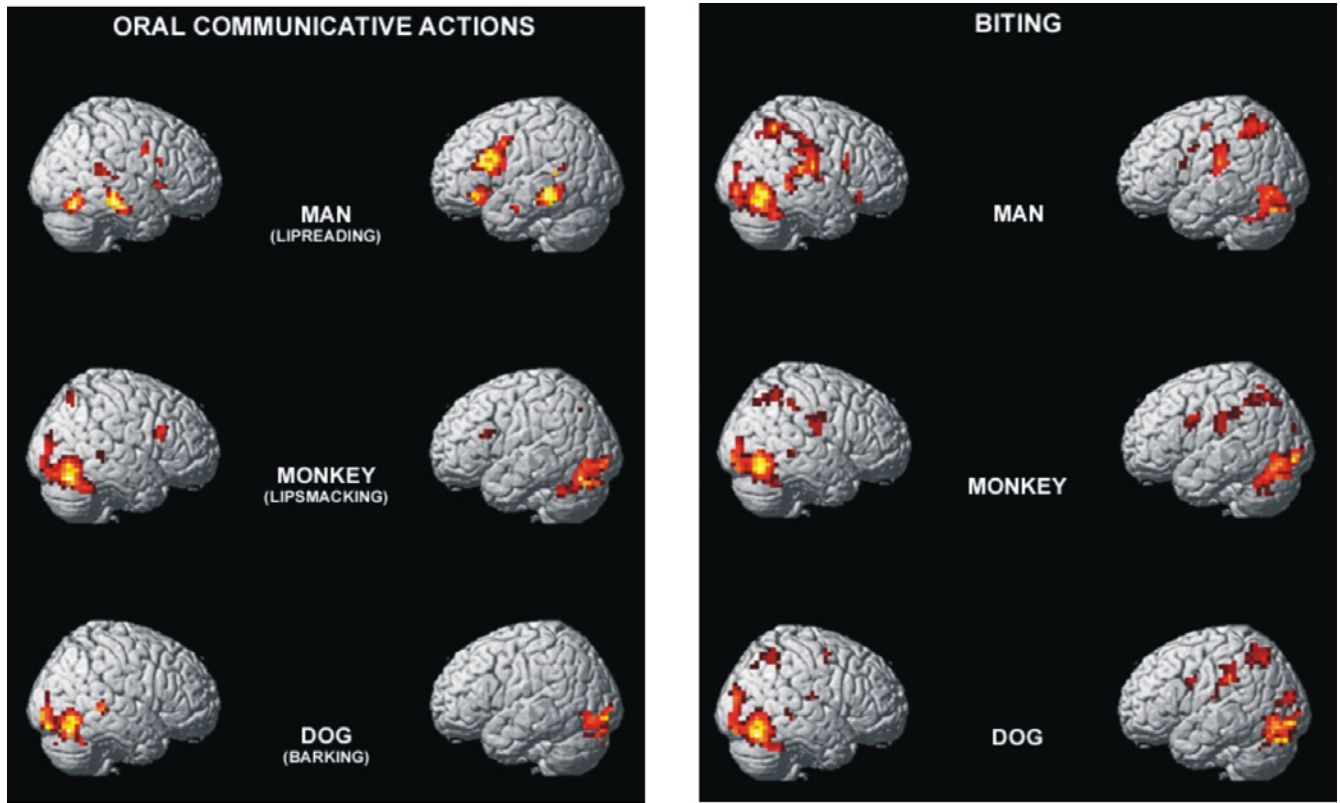


Figure2. Rizzolatti and Fadiga

Figure 2. Cortical areas activated during the observation of non-communicative (left panel) and communicative (right panel) actions performed by a man, a monkey and a dog.