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The mirror neuron system and action recognition

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Abstract

Mirror neurons, first described in the rostral part of monkey ventral premotor cortex (area F5), discharge both when the animal performs a goal-directed hand action and when it observes another individual performing the same or a similar action. More recently, in the same area mirror neurons responding to the observation of mouth actions have been also found. In humans, through an fMRI study, it has been shown that the observation of actions performed with the hand, the mouth and the foot leads to the activation of different sectors of Broca's area and premotor cortex, according to the effector involved in the observed action, following a somatotopic pattern which resembles the classical motor cortex homunculus. These results strongly support the existence of an execution-observation matching system (mirror neuron system). It has been proposed that this system is involved in action recognition. Experimental evidence in favor of this hypothesis both in the monkey and humans are shortly reviewed.
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1. Introduction

Action recognition is a fundamental step on which social behavior depends. Although numerous hypotheses have been forwarded to explain action recognition (see Barresi & Moore, 1996), two main theories may explain this cognitive function (Rizzolatti, Fogassi, & Gallese, 2001). The first one, often referred as the "visual hypothesis", maintains that action recognition relies on a visual analysis of all constituents of a specific action, that is a visual analysis of the effector involved, of the object on which the action is acted upon, and finally, of the context in which the action is going on. Inference about the interactions between all these elements visually described would allow the observer to understand and recognize actions performed by others. If this hypothesis were true, the neural substrates involved in action recognition would be the visual extrastriate areas, the inferotemporal lobe and the superior temporal sulcus region. The second one, referred as the "direct-matching hypothesis", maintains that one can recognize actions performed by others by mapping the observed action on his/her own motor representation of the observed action. According to this hypothesis, action observation automatically activates in the observer the same neural structures involved in the actual execution of the observed action. Since the result of the activation of these neural substrates during action execution is known, the activation of the same substrates during action observation would allow the observer, through an observation–execution matching mechanism, to understand what the actor is doing. This latter hypothesis has recently found a strong neurophysiological support in the discovery of the mirror neuron system. This review will focus on the organization of the mirror neuron system both in the monkey and humans, and on the experimental evidence of its involvement in action observation and recognition.

2. Mirror neuron system in the monkey

The rostral part of monkey ventral premotor cortex is called area F5, according to the nomenclature proposed by Matelli, Luppino, and Rizzolatti (1985). Electrophysiological studies have shown that in this area there is a motor representation of mouth and hand actions. Neurons related to hand actions discharge when the monkey executes specific goal-directed hand actions

such as grasping, holding, tearing and manipulating objects. It has been proposed that these neurons constitute a sort of "vocabulary" of hand actions (Rizzolatti et al., 1988). Very interestingly, part of these neurons discharge both when the monkey performs specific goal-directed hand actions and when it observes another monkey or an experimenter performing the same or a similar action (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996a). These neurons are called mirror neurons because the observed action seems to be "reflected", like in a mirror, in the motor representation for the same action of the observer. The congruence between the action motorically coded by the neuron and that triggering the same neuron visually may be very strict: in this case only the observation of an action which is identical to that coded motorically by the neuron can activate it. More often, this congruence is only broad; if this is the case, the observed and the executed action coded by the neuron match relatively to the goal of the action itself rather than to the single movements necessary to execute it. Some main features of mirror neurons should be underlined: during action observation they discharge only when a biological effector (a hand, for example) interacts with an object; if the action is performed with a tool the neuron does not discharge. Mirror neurons are not active also when the observed action is simply mimicked, that is executed in the absence of the object. Finally, mirror neurons do not discharge during the mere visual presentation of an object. The visual properties of mirror neurons resemble those of neurons found by Perrett et al. (1989) in the superior temporal sulcus region. These neurons, like mirror neurons, respond to the presentation of goal-directed hand actions, but also to walking, turning the head, moving the hand and bending the torso (for a review see Carey, Perrett, & Oram, 1997). Differently from mirror neurons described in area F5, neurons described in STS region do not seem to have a motor counterpart, although this aspect was never studied systematically.

Since their discovery, the hypothesis was forwarded that mirror neurons may play an important role both in action recognition and in motor learning (Jeannerod, 1994).

If mirror neurons are responsible for action recognition, then these neurons should discharge also when the whole sequence of the action is not completely seen by the monkey, provided that the goal of the observed action can be clearly inferred. A recent electrophysiological study (Umilta' et al., 2001) support the claim that mirror neurons may infer the goal of an action. In the experiment, two conditions were presented: in the first one (vision condition) the animal could see the whole sequence of a hand action, in the second one (hidden condition) the final part of the action was hidden from the sight of the monkey by means of a screen. In this last condition, however, the animal was shown that an object, for example a piece of food, was placed behind the screen which prevented the observation of the final part of the performed action. The results showed that mirror neurons discharge not only during the observation of action, but also when the final part of it is hidden. As a control, a mimicked action was presented in the same conditions. As expected, in this case, the neuron did not discharge neither in the full vision condition nor in the hidden condition.

Actions may be recognized also when presented acoustically, from their typical sound. Besides visual properties, a recent experiment has demonstrated that about 15% of mirror neurons also respond to the specific sound of an action. These neurons are called audio-visual mirror neurons (Koehler et al., 2002). Audio-visual mirror neurons could be used to recognize actions performed by other individuals even if only heard. It has been argued that these neurons code the action content, which may be triggered either visually or acoustically, thus representing a possible step for the acquisition of language. It is worth noting that for anatomical and physiological reasons area F5 is considered the monkey homologue of human Broca's area (Binkofski & Buccino, this issue; Petrides & Pandya, 1997; Rizzolatti & Arbib, 1998).

Up to now only mirror neurons related to hand actions were described. More recently it has been demonstrated that in area F5 there are also mirror neurons which discharge during the execution and observation of mouth actions. Most of mouth mirror neurons become active during the execution and observation of mouth ingestive actions such as grasping, sucking or breaking food. Some of them respond during the execution and observation of oral communicative actions such as lip-smacking (Ferrari, Gallese, Rizzolatti, & Fogassi, 2003).

There is at the moment no evidence for the presence of mirror neurons related to foot actions. Given the evidence in humans, strongly supporting the existence of a mirror neuron system related to a large number of body actions performed with the hand, the mouth and the foot (Buccino et al., 2001, see below), the existence of foot mirror neurons may not be excluded also in the monkey.

3. Mirror neuron system in humans

There is increasing evidence that a mirror neuron system also exists in humans. Converging data supporting this notion come from experiments carried out with neurophysiological, behavioral and brain imaging techniques.

3.1. Neurophysiological studies

The first evidence of the existence of a mirror neuron system in humans was provided by Fadiga, Fogassi,

Pavesi, and Rizzolatti (1995). During this experiment, single pulse transcranial magnetic stimulation (TMS) was delivered while subjects were observing an experimenter performing various hand actions in front of them. As control conditions, single pulse TMS was delivered during object observation, dimming detection and observation of arm movements. Motor evoked potentials (MEPs) were recorded from extrinsic and intrinsic hand muscles. Results showed that during hand action observation, but not in the other conditions, there was an increase of amplitude of motor evoked potentials recorded from those hand muscles, normally recruited when the observed action is actually performed by the observer. These results were recently fully confirmed by Strafella and Paus (2000). Furthermore, using the same technique, Gangitano, Mottaghy, and Pascual-Leone (2001) found that during the observation of hand actions not only there is an increase of MEPs amplitude in the muscles involved in the actual execution of the observed action, but MEPs are modulated in a fashion strictly resembling the time-course of the observed action. For example, the amplitude of MEPs recorded from the first dorsal interosseus muscle was modulated according to the degree of aperture in the observed finger over time. Taken together, these TMS data support the notion of a mirror neuron system coupling action execution and action observation both in terms of the muscles involved and the temporal sequence of the action.

Similar to these results are those obtained by Cochin, Barthelemy, Roux, and Martineau (1999) using quantified electroencephalography (qEEG). In this study Mu activity was blocked during both the observation and execution of various hand actions, when compared to rest. It is worth recalling that similar results were observed by Gastaut and Bert (1954), who noted the suppression of Mu activity in humans during cinematographic presentation of various actions. Results similar to those of Cochin et al. were obtained by Hari and coworkers (1998) using magnetoencephalography (MEG). In this study the authors found a suppression of 15–25 Hz activity, known to originate from the precentral motor cortex, during the execution and, to a less extent, during the observation of object manipulation. All these studies provide further evidence that observation and execution of action share common neural substrates.

3.2. Behavioral studies

Evidence in favor of the existence of a mirror neuron system also derives from neuropsychological studies, using behavioral paradigms. Brass, Bekkering, Wohlschlaeger, and Prinz (2000) investigated how movement observation could affect movement execution in a stimulus-response compatibility paradigm. Using a reaction time paradigm, they contrasted the role of sym-

bolic cues as compared to the observation of finger movements in the execution of finger movements. Subjects were faster to respond when the finger movement was the relevant stimulus. Moreover the degree of similarity between the observed and executed movement led to a further advantage in the execution of the observed movement. These results provide a strong evidence for an influence of the observed movement on the execution of that movement. Similar results were obtained by Craighero, Bello, Fadiga, and Rizzolatti (2002) in a study in which subjects were required to prepare to grasp as fast as possible a bar oriented either clockwise or counterclockwise, after presentation of a picture showing the right hand. Two experiments were carried out: in the first experiment the picture represented the final required position of the hand to grasp the bar, as seen through a mirror. In a second experiment, in addition to stimuli used in experiment one, other two pictures were presented, obtained rotating of 90° the hand shown in the pictures used in Experiment 1. In both experiments, responses of the subjects were faster when the hand orientation of the picture corresponded to that achieved by the hand at the end of action, when actually executed. Moreover the responses were globally faster when the stimuli were not rotated. The studies of Brass et al. and Craighero et al. may be interpreted as an evidence in favor of the theory of ideomotor action, first formulated by James (1890) and more recently revised by Greenwald (1970). According to this theory, building up an image of the sensory feedback related to a certain action is a fundamental step for the proper execution of that action. The prediction of this theory is that, when the execution of an action is guided by a stimulus, the more the stimulus is similar to the action, the more the execution of that action is facilitated. Interestingly, the strong interdependence between perception and action was emphasized also by Von Weizsaecker (1940), who formulated a theory of unity between action and perception, with both building a ''Gestaltkreis'' (literally translated, a form-circle). In the studies reported here the observation of an action facilitates the execution of that action. The theory of ideomotor action finds indeed a strong neurophysiological support in the existence of mirror neuron system, where, by definition the visual representation of an action and its motor counterpart are anatomically and functionally embedded.

3.3. Brain imaging studies

All the cited studies provide little, if any, insight on the localization of mirror neuron system in humans. This issue has been addressed by a number of brain imaging studies.

In an early positron emission tomography (PET) experiment aimed at identifying the brain areas active during action observation, Rizzolatti et al. (1996b),

comparing hand action observation with the observation of an object, found activation of Broca's area, the middle temporal gyrus and the superior temporal sulcus region. Broca's area is classically considered an area devoted to speech production. Recently, however, it has been demonstrated that in this area a motor representation of hand actions is also present (Binkofski & Buccino, this issue; Binkofski et al., 1999; Ehrsson et al., 2000). Given the homology between Broca's area and area F5 in the monkey, (where mirror neurons were originally discovered), this study provided the first evidence on the anatomical localization of the mirror neuron system for hand actions in humans. Using the same technique, both Decety et al. (1997) and Grèzes, Costes, and Decety (1998) searched for the brain foci related to the observation of meaningful and meaningless hand actions, respectively. Subjects performed either a passive observation or a delayed imitation task; both were compared to mere observation of static hand images. During the passive observation task, the same cortical circuits were active during both the observation of meaningful and meaningless actions, the active foci being the superior occipital gyrus, the occipito-temporal junction bilaterally, and the inferior parietal lobule and the precentral gyrus in the left hemisphere. During the delayed imitation task, the observation of both meaningful and meaningless actions led to the activation of common circuits involving the inferior and the superior parietal lobules and the premotor cortex bilaterally. Besides these common areas, observation of meaningful actions activation additionally evoked activity in the supplementary motor area and in the orbitofrontal cortex.

A recent fMRI study showed that in humans the mirror neuron system is complex and related to different body actions performed not only with the hand, but also with the foot and the mouth. Buccino et al. (2001) asked subjects to observe video-sequences presenting different actions performed with the mouth, the hand and the foot, respectively. The actions shown could be either transitive (the mouth/hand/foot was acted upon an object) or intransitive (the mouth/hand/foot action was performed without an object). The following actions were presented: biting an apple, grasping a cup, grasping a ball, kicking a ball, and pushing a brake. As a control, subjects were asked to observe a static image of each action.

The observation of both transitive and intransitive actions, compared to the observation of a static image of the same action, led to the activation of different regions in the premotor cortex and Broca's area, depending on the effector involved in the observed action. The different regions largely overlapped those where classical studies (Penfield & Rasmussen, 1950) had shown a somatotopically organized motor representation of the different effectors. Moreover, during the observation of transitive actions, distinct sectors in the inferior parietal lobule were active, including areas inside and around the intraparietal sulcus, with localization depending on the effector involved in the observed action. All activations found in this study are shown in Fig. 1.

On the whole, this study strongly supports the claim that, as in the actual execution of actions, during action observation different, somatotopically organized fronto-parietal circuits are recruited (Jeannerod, Arbib, Rizzolatti, & Sakata, 1995; Rizzolatti, Luppino, & Matelli, 1998). In this context, it is worth noting that mirror neurons, similar to those described in area F5, have recently been reported by Fogassi, Gallese, Fadiga, and Rizzolatti (1998) and Gallese, Fogassi, Fadiga, and Rizzolatti (2002) in the inferior parietal lobule of the monkey (area PF).

In contrast with the results of Grezes and Decety, those of Buccino et al. also show an involvement of the mirror neuron system during a mere observation task, thus suggesting that this system is indeed operating indipendent of the observer's cognitive strategy. The lack of parietal activation during the observation of transitive actions in the study of Rizzolatti et al. might be explained by the fact that in his study this condition was contrasted with the observation of graspable objects.

As previously stated, in the monkey the mirror neuron system is also activated when the animal observes an experimenter, a non-conspecific, performing the same or a similar action motorically coded by the neuron. A recent fMRI study (Buccino et al., in press) addressed whether we can recognize actions performed by members belonging to other species (non-conspecifics) using the same neural structures involved in the recognition of actions performed by conspecifics. In this study, normal subjects were asked to carefully observe different mouth actions performed by a man, a monkey and a dog, respectively. Two kinds of mouth actions were visually presented: biting a piece of food and oral communicative actions (human silent speech, monkey lip-smacking, and silent dog barking). The results showed that during the observation of biting, there is a clear activation of the pars opercularis of the inferior frontal gyrus and of the inferior parietal lobule, regardless of the species doing the action. During the observation of oral communicative mouth actions, a different pattern of activation was observed, this time depending on the species performing the action. During the observation of silent speech (human), there was a clear activation of Broca's area in both hemispheres, with a leftward asymmetry; during the observation of lip-smacking (monkey) there was only a small bilateral activation in the pars opercularis of Broca's area, with no clear asymmetry between the two hemispheres. Finally during the observation of silent dog barking no activation was found in Broca's area, but activation was present only in the right superior temporal sulcus region. The results of the
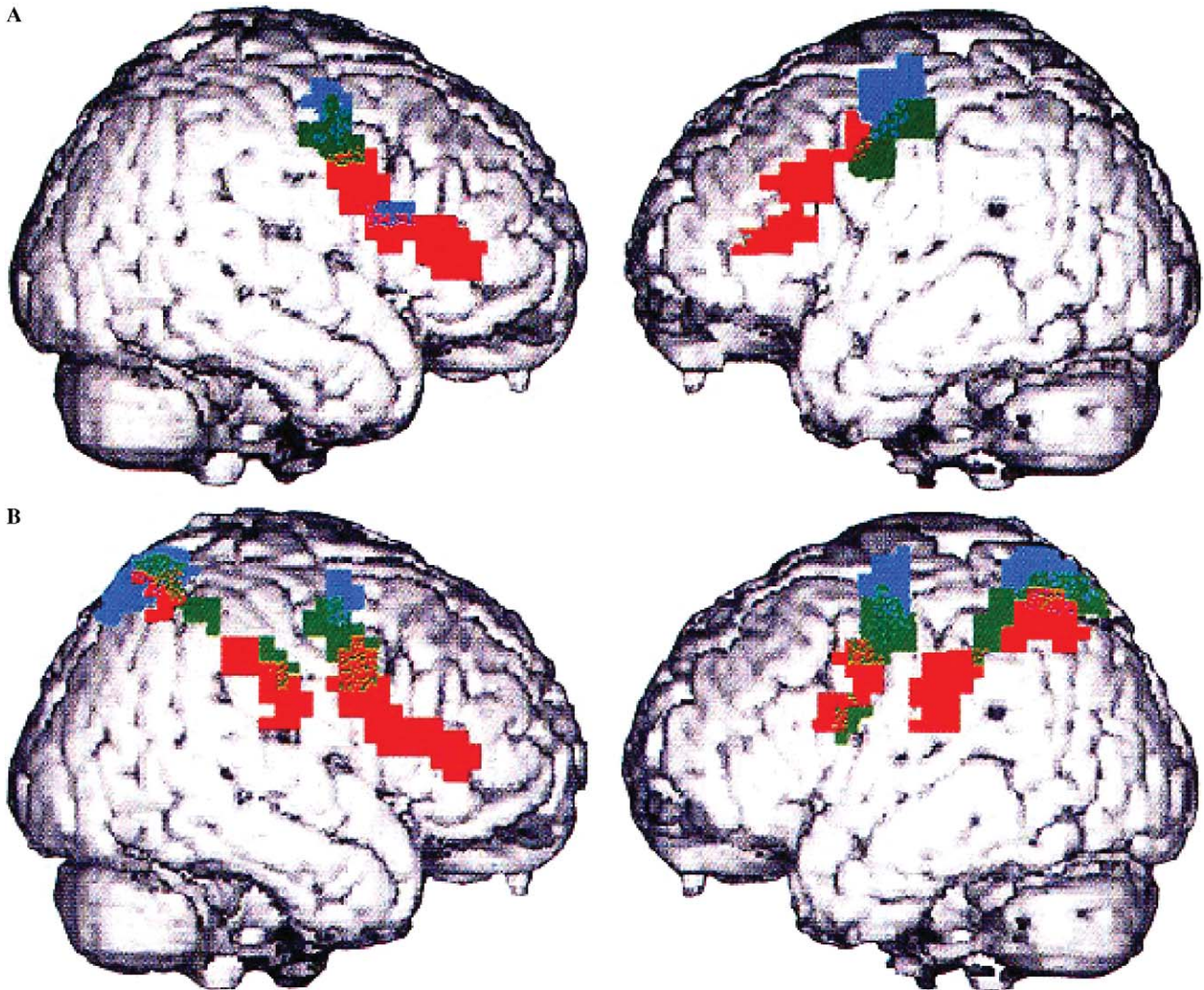
Fig. 1. Somatotopically organized activations in premotor and parietal cortices during action observation, projected on the lateral surface of Montreal Neurological Institute (MNI) standard brain. (A) Observation of intransitive actions. (B) Observation of transitive actions. Red: activation found during observation of mouth actions; green: activation found during observation of hand actions; blue: activation found during observation of foot actions. From Buccino et al. (2001).

experiment strongly suggest that action performed by other individuals, including non-conspecifics, may be recognized in two different ways: for actions like biting or silent speech reading, there is a motor resonance of the cortical circuits involved in the actual execution of the observed actions. In other words their recognition relies on the mirror neuron system. For actions like barking, this resonance is missing. In the first case there is a "personal" knowledge of the action observed, in the sense that it is mapped on the observer's motor repertoire and therefore the observer has a direct, personal experience in motor terms of it (e.g., I recognize it because I am able to do the same action I am looking at). In the second case, although the viewed actions are still recognized as biological motion (as suggested by the activation of the STS region), personal knowledge about these actions is lacking because the observer has no di-

rect experience of the observed action in motor terms (e.g., I can approximately imitate a dog barking, but, as a matter of fact, I am not able to do it). These results are coherent with brain imaging studies which have shown that the mirror neuron system is not involved during the observation of actions performed by non-biological agents (Perani et al., 2001) or during the observation of biological motion defined by point-light figures (Grossman et al., 2000; Vaina, Solomon, Chowdhury, Sihna, & Belliveau, 2001).

In conclusion, converging data suggest that we can recognize a large variety of actions performed by other individuals, including those belonging to other species, simply by matching the observed actions onto our own motor system. The neural substrate of this direct-matching is the mirror neuron system, which therefore may represent the biological basis not only for social

interactions, but also, as recently proposed, for empathy with other people and the attribution of intentions to others (Gallese, 2003). Even more interesting for the aim of the present paper, the hypothesis has been forwarded that the mirror neuron system may constitute a necessary precursor to the capacity to imitate, fundamental for the human culture, and to the acquisition of language (Rizzolatti & Arbib, 1998; Rizzolatti, Fadiga, Fogassi, & Gallese, 2002). The recent finding of mirror neurons related to oral communicative actions in the monkey (Ferrari et al., 2003), the activation of Broca's area during the observation of silent speech in humans (Buccino et al., in press) and the evidence that the amplitude of MEPs recorded from lip and tongue muscles increases during speech listening, when the correspondent motor areas are stimulated by means of TMS (Fadiga, Craighero, Buccino, & Rizzolatti, 2002; Watkins, Strafella, & Paus, 2003), strongly support this view.

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