ORIGINAL ARTICLE

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The mirror neuron system and its function in humans

Mirror neurons are a particular type of neurons that discharge when an individual performs an action, as well as when he/she observes a similar action done by another individual. Mirror neurons have been described originally in the premotor cortex (area F5) of the monkey. Subsequent studies have shown that they are present also in the monkey inferior parietal lobule (Rizzolatti et al. 2001).

In the human brain, evidence for mirror neurons is indirect, but, although there is no single-neuron study showing the existence of mirror neurons, functional imaging studies revealed activation of the likely homologue of monkey area F5 (area 44 and the adjacent ventral area 6) during action observation (see Rizzolatti and Craighero 2004). Furthermore, magnetoencephalography (Hari et al. 1998) and EEG (Cochin et al. 1999) have shown activation of motor cortex during observation of finger movements. Very recently, alpha rhythm desynchronization in functionally delimited language and hand motor areas was demonstrated during execution and observation of finger movements in a patient with implanted subdural electrodes (Tremblay et al. 2004).

What is the functional role of the mirror neurons? Various hypotheses have advanced: action understanding, imitation, intention understanding, and empathy (see Rizzolatti and Craighero 2004; Gallese et al. 2004). In addition, it has been suggested that mirror-neuron system is the basic neural mechanism from which language developed (Rizzolatti and Arbib 1998).

It is my opinion that the question of which is *the* function of the mirror neurons or of the mirror-neuron system is ill posed. Mirror neurons do not have a specific functional role. The properties of mirror neurons indicate that primate brain is endowed with a mechanism mapping the pictorial description of actions, carried out in the higher order visual areas onto their motor counterpart. This matching mechanism may underlie a variety of functions, depending on what aspect of the observed action is coded, the species considered, the circuit in which mirror neurons are included, and the connectivity of the mirror-neuron system with other systems.

Let us examine first action understanding, the original hypothesis that has been proposed for explaining the functional role of the mirror system (Gallese et al. 1996; Rizzolatti et al. 1996). It might sound bizarre that in order to recognize an action, one should activate the motor system. As a matter of fact, this is not so strange. A mere visual perception, without involvement of the motor system would only provide a description of the visible aspects of the movements of the agent. It would not give, however, information on the intrinsic components of the observed action, on what means doing it, and of the links of the observed actions with other actions related to it. To put the observed action into a motor semantic network is simply a necessity, if one has to understanding what the observed action is really about.

Thus, the activation of the parieto-premotor mirror circuit is fundamental to provide the observer with a real comprehension of the observed action. This "real" action understanding is present in both monkeys and humans. On the top of it, other functions can be built, some of which are present only in humans. One of them is imitation.

Mirror-neuron system provides a motor copy of the observed actions. Thus, it appears to be the ideal mechanism for *imitation*. Yet, the monkeys that have a mirror system possess this capacity in a very limited form, if they have it at all (Visalberghi and Fragaszy 2001). So is the mirror system involved in imitation and, if this is the case, why monkeys do not use it for imitation?

The answer to the first question is yes. There is clear evidence that, in humans, mirror-neuron system is involved in immediate repetition of actions done by others

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(Iacoboni et al. 1999), as well as in imitation learning (Buccino et al. 2004; Nishitani and Hari 2000). As far as the lack of imitation in monkeys is concerned, a possible explanation can be found in the properties of the mirror neuron system in the two species. In monkeys, mirror neurons respond during the observation of goal directed actions; in humans, mirror system is also activated by intransitive, meaningless movements (Fadiga et al. 1995). Thus, the monkey mirror system appears to be tuned to describe the goal of actions, but not to code the way in which this goal is achieved. Monkeys understand the goal of the observed action and can emulate it (i.e., reach its goal), but have a mirror machinery too primitive to code the details of the observed action. They cannot therefore replicate the observed action (Rizzolatti and Craighero 2004).

Recent brain imaging experiments showed that an important role in imitation learning is played by the prefrontal lobe (Buccino et al. 2004). This lobe and area 46, in particular, appears to be the structure that combines elementary motor acts (e.g., specific finger movements) into more complex motor patterns. Considering the large expansion of the frontal lobe in humans, it is possible that the monkey frontal lobe does not possess a machinery sufficient to perform this combinatory activity on the mirror-neuron system.

There are two distinct information that one can get observing an action done by another individual. One is "what" the actor is doing; the other is "why" the actor is doing it. If we see, e.g., a girl grasping an apple, we understand that she is grasping an object. Often, we can also understand, in addition, why she is doing it, i.e., we can understand her *intention*. We can infer if she is grasping the apple for eating it, or for putting it into a basket. The hypothesis that mirror neurons are involved in intention understanding has been proposed some years ago (Gallese and Goldman 1998). Only recently, however, this hypothesis has been experimentally tested.

In an fMRI experiment, normal volunteers watched three types of stimuli: grasping hand actions without a context, context only (scenes containing objects), and grasping hand actions executed in different contexts. In the latter condition, the context allowed the subject to infer the intention of the grasping action. Actions embedded in contexts, compared with the other two conditions, yielded selective activation of area 44 and the adjacent sector of the ventral premotor cortex. This indicates that mirror areas, in addition to action understanding, also mediate the understanding of others' intention (Iacoboni et al. 2005).

The functions mediated by the mirror neurons depend on the anatomy and physiological properties of the circuit in which these neurons are located. Actions studied in the early mirror-neuron studies were actions devoid of emotional content. Accordingly, activations were found in circuits related to motor action control (parieto-premotor circuits). Recently, evidence has been found that the mirror mechanism is also involved in *empathy*, i.e., in the capacity of feeling the same emotions that others feel. In an fMRI experiment, participants were exposed, in one condition, to disgusting odorants and, in another, presented with short movie clips showing individuals displaying a facial expression of disgust. Activations produced by disgusting stimuli were contrasted with activation obtained with neutral stimuli. It was found that the exposure to disgusting odorants specifically activates the anterior insula and the anterior cingulate. Most interestingly, the observation of the facial expression of disgust activated the *same* sector of the anterior insula (Wicker et al. 2003). In close agreement with these findings are the data obtained in another fMRI experiment that showed activation of the anterior insula during the observation and imitation of facial expressions of basic emotions (Carr et al. 2003).

These data strongly suggest that the insula contains a neural population active both when an individual directly experiences disgust and when this emotion is triggered by the observation of the facial expression of others. It has been proposed, in analogy with action understanding, that feeling emotions is due to the activation of circuits that mediate the corresponding response, and namely, in this case, viscero-motor responses (Gallese et al. 2004).

Finally, the hypothesis has been advanced that the mirror mechanism represents the basic mechanism from which language evolved (Rizzolatti and Arbib 1998). Conceptually, the view that speech evolved from gestural communication is not new (see for modern versions of this idea, Armstrong et al. 1995; Corballis 2002). The theory of Rizzolatti and Arbib (1998) has, however, a fundamental asset. It is the first theory that indicates a neurophysiological mechanism that may create a common, non-arbitrary link between communicating individuals (parity requirement).

It is obvious that mirror mechanism does not explain by itself the enormous complexity of speech. Yet, it solves one of the fundamental difficulties for understanding language evolution that is how what is valid for the sender of a message become valid also for the receiver. Hypotheses and speculations on the various steps that have led from monkey mirror system to language have been advanced recently both Arbib (2002), and Rizzolatti and Craighero (2004). The interested reader is referred to these articles for information on this topic.

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