

Mirror neurons

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Mirror neurons represent a distinctive class of neurons that discharge both when the monkey executes a motor act and when it observes another individual (a human being or another monkey) performing the same or a similar motor act (Figure 1). These neurons do not discharge in response to the simple presentation of food or of other interesting objects. They also do not discharge, when the monkey observes hand actions mimicked without the target object. Thus, the effective visual stimulus is the observation of a hand interacting with an object (Gallese et al. 1996, Rizzolatti et al. 1996a).

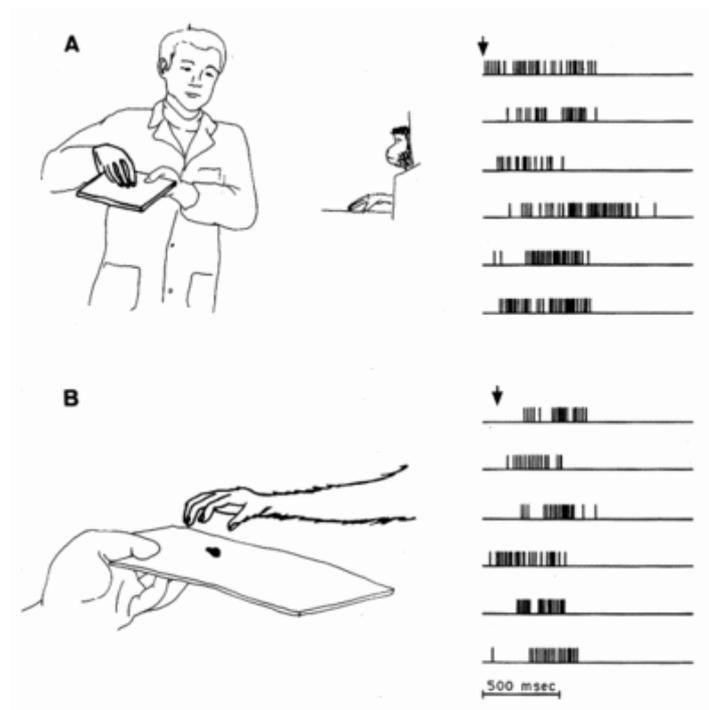


Figure 1: Example of a F5 mirror neuron selectively discharging (A) during observation of a grasping movement done by the experimenter and (B) during monkey grasping movements. Arrows denote the onset of the movement. Six trials are shown for each condition.

Originally discovered in a subdivision of the monkey's premotor cortex, area F5, mirror neurons have later been also found in the inferior parietal lobule (IPL, Rizzolatti et al. 2001, Fogassi et al. 2005) (Figure 2). IPL receives a strong input from the cortex of the superior temporal sulcus (STS), a region known to code biological motion (Jellema et al. 2002), and sends output to ventral premotor cortex including area F5. Note that, although STS responds to the observation of actions done by others, it is not endowed with motor properties. Thus, the cortical mirror neuron system is formed by two main regions:

1. the ventral premotor cortex and

2. the rostral part of the inferior parietal lobule.

Neurophysiological (EEG, MEG, and TMS), and brain-imaging (PET and fMRI) experiments provided strong evidence that a fronto-parietal circuit with properties similar to the monkey's mirror neuron system is also present in humans (Rizzolatti and Craighero 2004). As in the monkey the mirror neuron system is constituted of IPL and a frontal lobe sector formed by the ventral premotor cortex plus the posterior part of the inferior frontal gyrus (IFG) (Figure 3).

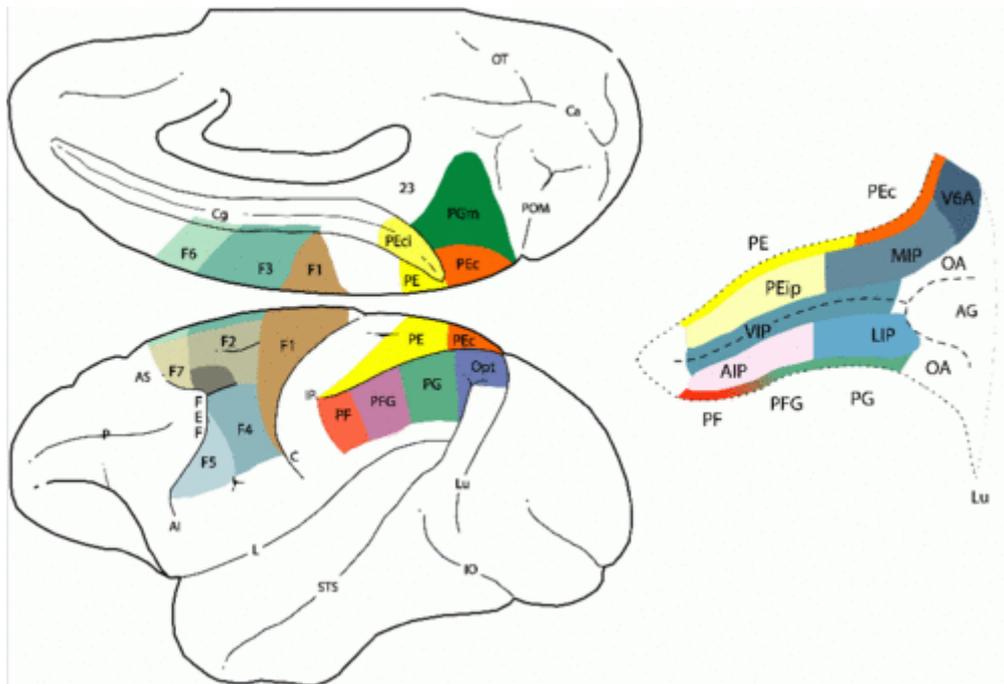


Figure 2: Mesial and lateral views of the macaque brain showing the cytoarchitectonic parcellation of the frontal motor cortex (areas indicated with F and Arabic numbers) and of the parietal lobe (areas indicated with P and progressive letters). Areas buried within the intraparietal sulcus are shown in an unfolded view of the sulcus. AIP, anterior intraparietal area; As, superior arcuate sulcus; Ai inferior arcuate sulcus; C, central sulcus; Ca, calcarine fissure; CG, cingulate cortex; FEF, frontal eye field; IP, intraparietal sulcus; L, lateral sulcus; LIP, lateral intraparietal area; MIP, medial intraparietal area; Lu, lunate sulcus; P, principal sulcus POs, parieto-occipital sulcus; STS, superior temporal sulcus.

Functional roles of the mirror neuron system

What might be the functional role of the mirror neuron system? A series of hypotheses such as action understanding, imitation, intention understanding, and empathy have been put forward to explain the functional role of the mirror neurons. In addition to these, it has also been suggested that the mirror neuron system represents the basic neural mechanism from which language evolved.

The question, however, of what is the function of the mirror neuron system is probably an ill posed question. Mirror neurons do not have a unique functional role. Their properties indicate, rather, that they represent a mechanism that maps 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.

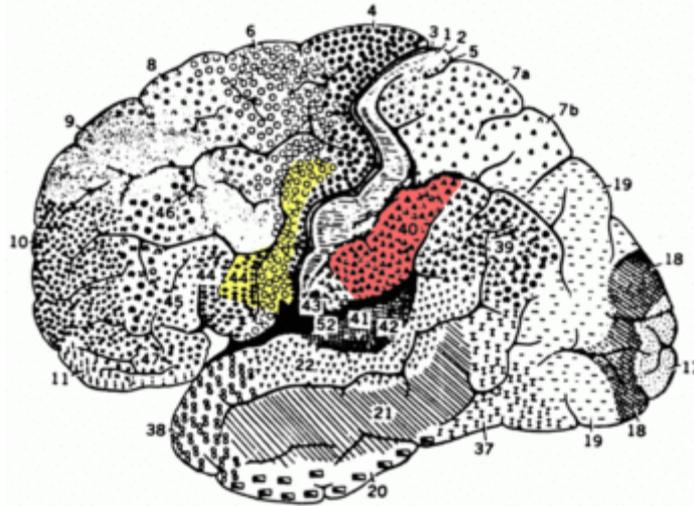


Figure 3: Mirror neuron system in humans. Lateral view of human brain showing the areas (colored) that form the mirror neuron system.

Action understanding and imitation

The original hypothesis on the functional role of mirror neuron system was that of action understanding (Rizzolatti et al. 2001). It may sound bizarre that in order to recognize an action, one should activate the motor system. However, 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. It would not give, however, information on the intrinsic components of the observed action, on what it means to do the action, and on the links between the observed action and other actions related to it. This can be achieved only if the observed action is mapped onto the motor system of the observer. Thus, the activation of the mirror circuit is essential to provide the observer with a real experiential comprehension of the observed action. This comprehension links the observer of the action with its agent, creating a rudimentary form of social interactions. On top of this function, other functions can be built, some of which are present only in humans.

From this perspective, mirror neurons could represent a "core mechanism" from which other functions branched off. One of these is imitation, that is the ability to replicate an observed action already present in the observer motor repertoire or to learn a new motor action. The mirror neuron system, by providing motor copies of the observed actions, appears to be the ideal mechanism for imitation. Indeed, there is clear evidence that mirror neuron system is involved both in immediate repetition of actions done by others (Iacoboni et al. 1999) and in imitation learning (Buccino et al. 2004).

While immediate repetition of an observed action is carried out by the mirror system itself, imitation learning requires the intervention of the prefrontal lobe (Iacoboni et al. 1999). This lobe (area 46 in particular) combines elementary motor acts into more complex motor patterns.

Intention understanding

There are two distinct series of 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, for example, 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, that is we can understand her intention. We can infer if she is grasping the apple for eating it, or for putting it into a basket. Although the hypothesis that mirror neurons are involved in intention understanding has been proposed several years ago (Gallese and Goldman 1998), only recently, however, this hypothesis has been supported by an fMRI experiment. In this experiment volunteers were presented with hand actions without a context and hand actions executed in contexts that allowed them to understand the intention of the action agent. The main result of the study was the demonstration that actions embedded in contexts yielded selective activation of the mirror neuron system. This indicates that mirror areas, in addition to action understanding, also mediate the understanding of others' intention (Iacoboni et al. 2005).

These data indicate that the mirror neuron system is involved in intention understanding, without providing, however, information on the specific mechanisms underlying it. In order to elucidate these mechanisms monkeys were trained to perform two actions with different goals (Fogassi et al. 2005).

- In the first, the monkey had to grasp an object in order to place it into container,
- in the second it had to grasp a piece of food to eat it.

The initial motor acts, reaching and grasping, were identical in the two conditions, while the final goal of the two actions was different. The activity of single neurons was recorded from the inferior parietal lobule (IPL). The results showed that many of IPL neurons discharge selectively when the monkey executes a given motor act (e.g. grasping). Very interestingly, most of them fire only when the coded motor act is followed by a subsequent specific motor act (e.g. placing).

Some of these "action-constrained" motor neurons had mirror properties and selectively discharged during the observation of motor acts when these were embedded in a given action (e.g., grasping-for-eating but not grasping-for-placing). Thus, the activation of IPL action-constrained mirror neurons give information not only about, but also on why grasping is done (grasping-for-eating or grasping-for placing). This specificity allowed the observer not only to recognize the observed motor act, but also to code what will be the next motor act of the not-yet-observed action: In other words to understand the intentions of the action's agent. It has been suggested that there is a link between autism and mirror neuron system. According to this view, the inability of autistic children to relate to people and life situations in the ordinary way depends on a lack of a normally functioning mirror neuron system. Recent neurophysiological and brain imaging studies provided evidence in favor of this hypothesis (Ramachandran and Oberman 2006; Dapretto et al. 2006).

It is generally assumed that the primary deficit in intention understanding found in autistic children, is due to damage of the mirror system as the system responsible for understanding the actions of others. However, one may wonder whether the primary deficit in autism lies indeed in the incapacity to understand others or rather in a more basic deficit in the organization of the motor chains. In other words, the fundamental deficit in autistic children resides in the incapacity to organize their own intentional motor behavior.

Emotions and empathy

Functions mediated by mirror neurons depend on the anatomy and physiological properties of the circuit in which these neurons are located. Actions studied in the initial mirror neuron studies were actions without an emotional content. Accordingly, activations were found in circuits related to motor action control (parieto-premotor circuits). Recent evidence suggests that the mirror mechanism is also involved in empathy, that is 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, to short movie clips showing individuals displaying a facial expression of disgust. 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. Similar data have been obtained for felt pain and during the observation of a painful situation in which was involved another person loved by the observer (Singer 2006, Saarela et al. 2006). Taken together, these experiments suggest that feeling emotions is due to the activation of circuits that mediate the corresponding emotional responses (Gallese et al. 2004).

Language evolution

Humans mostly communicate by sounds. Sound-based languages, however, do not represent the only natural way for communicating. Languages based on gestures (signed languages) represent another form of complex, fully-structured communication system. Nonetheless, the fact that signed languages represent a fully structured communication system has not changed the view, which many share, that speech is the only natural human communication system and that the evolutionary precursor of human speech consists of animal calls. The argument goes as follows: Humans emit sound to communicate, animals emit sounds to communicate, therefore human speech evolved from animal calls.

The logic of this syllogism is, however, rather shaky. Its weakness becomes apparent when one examines animal calls and human speech more closely. First, the anatomical structures underlying primate calls and human speech are different. Primate calls are mostly mediated by the cingulate cortex and by deep, diencephalic and brain stem structures (Jürgens 2002). In contrast, the circuits underlying human speech are formed by areas located around the Sylvian fissure, including the posterior part of IFG.

Second, speech in humans is not, or is not necessarily, linked to emotional behavior, whereas animal calls are. Third, speech is mostly a dyadic, person-to-person communication system. In contrast, animal calls are typically emitted without a well-identified receiver. Fourth, speech is endowed with combinatorial properties that are absent in animal communication. Finally, humans do possess a "call" communication system like that of non-human primates and its anatomical location is similar. This system mediates the utterances that humans emit when in

particular emotional states (cries, yelling, etc.). These utterances are preserved in patients with global aphasia.

If not animal calls, what could be the origin of human speech? An alternative hypothesis is that the path leading to speech started with gestural communication (for a modern version of this idea see Armstrong 1995; Corballis 2002). According to this theory, the initial communicative system in primate precursors of modern humans was based on simple, elementary gesturing. Sounds were then associated with the gestures and became progressively the dominant way of communication.

The discovery of mirror neurons provided strong support for the gestural theory of speech origin. Mirror neurons create a direct link between the sender of a message and its receiver (Rizzolatti and Arbib 1998). Thanks to the mirror mechanism, actions done by one individual become messages that are understood by an observer without any cognitive mediation. The observation of an individual grasping an apple is immediately understood because it evokes the same motor representation in the parieto-frontal mirror system of the observer. On the basis of this fundamental property of mirror neurons and the fact that the observation of actions like hand grasping activates the caudal part of IFG (Broca's area), Rizzolatti and Arbib (1998) proposed that the mirror mechanism is the basic mechanism from which language evolved. In fact, the mirror mechanism solved, at a initial stage of language evolution, two fundamental communication problems: parity and direct comprehension. Thanks to the mirror neurons, what counted for the sender of the message also counted for the receiver. No arbitrary symbols were required. The comprehension was inherent in the neural organization of the two individuals.

It is obvious that the 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 recently advanced (Arbib 2005).

References

- Arbib M.A. 2005 From monkey-like action recognition to human language: an evolutionary framework for neurolinguistics. *The Behavioral and brain sciences*. 2:105-24
- Armstrong AC, Stokoe WC, Wilcox SE. 1995. *Gesture and the nature of language*. Cambridge, UK: Cambridge University Press.
- Buccino G, Vogt S, Ritzl A, Fink GR, Zilles K, Freund HJ, Rizzolatti G 2004. Neural circuits underlying imitation of hand actions: an event related fMRI study. *Neuron* 42:323-34.
- Carr L, Iacoboni M, Dubeau MC, Mazziotta JC, Lenzi GL 2003 Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. *Proc. Natl Acad. Sci. U.S.A.* 100: 5497-5502.
- Corballis MC. 2002. *From hand to mouth. The origins of language*. Princeton: Princeton University Press, 257 pp.

- Dapretto M, Davies MS, Pfeifer JH, Scott AA, Sigman M, Bookheimer SY, and Iacoboni M. 2006. Understanding emotions in others: Mirror neuron dysfunction in children with autism spectrum disorders. *Nature Neuroscience*, 9,28-30.
- Fogassi L., Ferrari P.F., Gesierich B., Rozzi S., Chersi F. and Rizzolatti G. 2005. Parietal Lobe: from Action Organization to Intention Understanding. *Science*, 308: 662-7
- Gallese V, Fadiga L, Fogassi L, Rizzolatti G. 1996. Action recognition in the premotor cortex. *Brain* 119:593-609
- Gallese V., Goldman A. 1998. Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Sciences*, 12:493-501,
- Gallese V., Keysers C. and Rizzolatti G. 2004 A unifying view of the basis of social cognition. *Trends in Cognitive Sciences*, 8: 396-403
- Iacoboni M., Molnar-Szakacs I., Gallese V., Buccino G., Mazziotta J.C., Rizzolatti G. 2005 Grasping the intentions of others with one's own mirror neuron system. *PLoS biology*, 3, e79
- Iacoboni M, Woods RP, Brass M, Bekkering H, Mazziotta JC, Rizzolatti G. 1999. Cortical mechanisms of human imitation. *Science* 286:2526-8.
- Jellema T, Baker CI, Oram MW, Perrett DI. 2002. Cell populations in the banks of the superior temporal sulcus of the macaque monkey and imitation. In *The imitative mind. Development, evolution and brain bases*, ed., AN Melzoff, W Prinz. Cambridge: Cambridge University Press.
- Jürgens, U. 2002. Neural pathways underlying vocal control. *Neuroscience and Biobehavioral Review*, 26, 235-258.
- Ramachandran V.S., Oberman L.M. 2006 Broken mirrors: a theory of autism. *Scientific American*, 5: 62-9
- Rizzolatti G, Arbib MA. 1998. Language within our grasp. *Trends Neurosci.* 21:188-94
- Rizzolatti G, Fadiga L, Fogassi L, Gallese V. 1996a. Premotor cortex and the recognition of motor actions. *Cogn. Brain Res.* 3:131-41
- Rizzolatti G, Fogassi L, Gallese V. 2001. Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat. Rev. Neurosci.* 2:661-70.
- Rizzolatti G., Craighero L. 2004 The Mirror-Neuron System. *Annual Rev. Neurosci.* 27 169-192
- Saarela MV, Hlushchuk Y, Williams AC, Schurmann M, Kalso E, Hari R. 2006 The Compassionate Brain: Humans Detect Intensity of Pain from Another's Face. *Cerebral cortex*
- Singer T. 2006 The neuronal basis and ontogeny of empathy and mind reading: review of literature and implications for future research. *Neuroscience and biobehavioral reviews.* 6: 855-63.
- Wicker B., Keysers C, Plailly J, Royet JP, Gallese V, Rizzolatti G.. (2003) Both of us disgusted in my insula: The common neural basis of seeing and feeling disgust. *Neuron* 40, 655-664.