

Mirror Neuron System: Basic Findings and Clinical Applications

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In primates, ventral premotor and rostral inferior parietal neurons fire during the execution of hand and mouth actions. Some cells (called *mirror neurons*) also fire when hand and mouth actions are just observed. Mirror neurons provide a simple neural mechanism for understanding the actions of others. In humans, posterior inferior frontal and rostral inferior parietal areas have mirror properties. These human areas are relevant to imitative learning and social behavior. Indeed, the socially isolating condition of autism is associated with a deficit in mirror neuron areas. Strategies inspired by mirror neuron research recently have been used in the treatment of autism and in motor rehabilitation after stroke.

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A recent neurophysiological discovery has sparked interest on how the primate brain codes the actions of others. In monkeys, ventral premotor and rostral inferior parietal neurons fire when the animal performs hand and mouth actions, but also when the animal is simply observing another individual performing the same actions. These cells, called *mirror neurons*, appear to provide a relatively simple neural mechanism for action recognition. This neurophysiological discovery in macaques has inspired several brain imaging experiments in humans. The human brain imaging experiments have demonstrated neural systems with mirroring properties in human brain regions anatomically comparable to the monkey's mirror neuron areas (Fig 1). This article discusses the basic neurophysiological findings in primates, the main brain imaging results in humans, and the most important clinical applications of mirror neuron research.

Macaque Frontoparietal Systems for Sensorimotor Behavior

The parietal and frontal lobe of the macaque brain form a massive and parallel cortical circuitry concerned with sensorimotor behavior. Several frontoparietal circuits have been identified in anatomic and physiological terms. The general architecture is as follows: a parietal and a frontal area are robustly and reciprocally connected, whereas having weaker anatomic connections with other parietal and frontal areas. This architecture allows specialized yet flexible circuits for senso-

rimotor behavior, in which parietal areas provide visual and somatosensory input to frontal areas.^{1–3}

The anatomic and physiological organization of primate frontoparietal systems has previously informed and inspired research on neurological patients. For instance, our understanding of the neural mechanisms producing dissociable unilateral neglect for near and far space^{4,5} relies on two well-defined and independent frontoparietal systems for extrapersonal and peripersonal space. The system for “far space” is composed of lateral intraparietal area and frontal eye field, whereas the system for “near space” is composed of ventral intraparietal area and ventral premotor area F4. Experimental lesions in these two systems produce dissociable extrapersonal (far space) and peripersonal (near space) neglect.⁶ The properties of neurons within these systems clearly suggest spatial “pragmatic” maps based on the kind of actions that extrapersonal and peripersonal space afford.^{7–10}

The visuomotor transformations required by grasping behavior are implemented by a frontoparietal system composed of anterior intraparietal area and ventral premotor area F5.¹¹ Area F5 is composed of two main sectors, one in the bank of the arcuate sulcus (F5ab) and the other on the convexity behind the sulcus (F5c). F5c is connected with rostral inferior parietal areas PF and PFG.¹² Mirror neurons are located within the frontoparietal system composed of F5c and PF/PFG.

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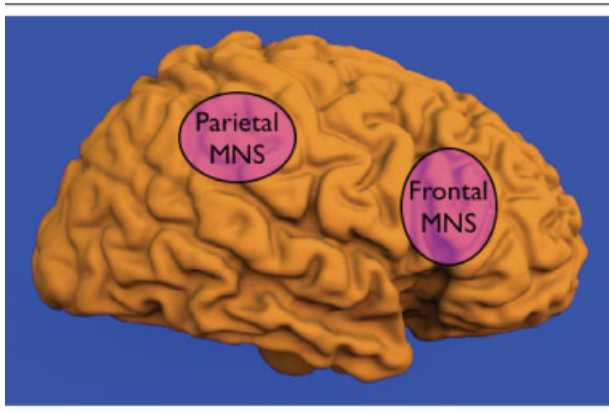


Fig 1. Schematic view of the frontal and parietal component of the human mirror neuron system (MNS). (Modified from Iacoboni,⁶⁶ by permission.)

Mirror Neurons: Neurophysiology

The discharge of mirror neurons is associated with object-oriented hand actions such as grasping, holding, tearing, and manipulating,^{13–15} and mouth actions of two main types, ingestive and communicative.¹⁶ The defining feature of mirror neurons is that they fire when the animal is performing these actions, but also, although with slightly weaker discharge compared with motor execution, when the monkey simply observes another individual, either a human experimenter or a conspecific, performing those actions.

Mirror neurons are divided in two main categories: strictly congruent and broadly congruent. *Strictly congruent* mirror neurons, about one third of all mirror neurons, fire for exactly the same action, either executed or observed. *Broadly congruent* mirror neurons represents approximately two thirds of all mirror neurons and fire for actions that are either logically related (such as grasping and bringing to the mouth)¹³ or that achieve the same goal.^{14,17} The fact that broadly congruent mirror neurons outnumber strictly congruent mirror neurons suggests that mirror neurons are not simply concerned with mirroring others, but they rather facilitate social interactions in which individuals often perform complementary actions to achieve a common goal.¹⁸

Mirror neurons appear to implement a fairly sophisticated and rather abstract coding of the actions of others. For instance, they distinguish between a hidden grasping action and a hidden pantomime of the same action.¹⁹ This property was shown by the following experiment. Monkeys observed an experimenter grasping an object and pantomiming the same action. Mirror neurons fired when the experimenter grasped, but not when the experimenter pantomimed. In another experimental condition, monkeys were shown a graspable object on a table. The sight of the object was then occluded with a screen. Monkeys observed the experi-

menter reaching behind the screen. Even though the completion of the grasping action was occluded by the screen, mirror neurons fired at the hidden action. In a final experimental condition, the monkeys were shown a bare table with no graspable object on it. The screen occluded the sight again, and the experimenter reached behind the screen. Even though this experimental condition was at this point visually identical to the previous one, the prior knowledge of the absence of graspable objects on the table caused the mirror neurons not to fire. This property of mirror neurons is probably the neural basis of our understanding of the actions of other people that we cannot completely see, which are partially occluded.

Another property of mirror neurons is that they fire at the sound associated with an action, such as breaking a peanut, tearing paper, and so on, even though the action is not seen.^{20,21} This property suggests that mirror neurons provide a multimodal, fairly abstract coding of the actions of other people.

The same action, however, can be associated with different intentions. Do mirror neurons code the action, or rather the associated intention? In a recent study, monkeys were trained to grasp and then place an object (and even a piece of food) in a container. The monkeys were also recorded when grasping and subsequently eating the food. Approximately one third of recorded neurons fired equivalently for grasping to place and grasping to eat. Two thirds of recorded neurons, however, discharged differently for grasping to place and grasping to eat. The majority of cells discharged more strongly for grasping to eat.

The same neurons were also recorded while the monkeys were observing a human experimenter either grasping to place (the presence of a container signaled this intention) or grasping to eat (the absence of the container cued the intention to eat). A subset of the neurons coding grasping actions demonstrated mirror properties, firing during action observation. Critically, these cells also mirrored the pattern of discharge during grasping execution. For instance, neurons that discharged more for grasping to eat during motor execution also discharged more for observed grasping actions in absence of the container, an absence that signaled the intention to eat. Likewise, neurons that discharged more for grasping to place during motor execution also discharged more for observed grasping in presence of the container, a presence that signaled the intention to place.²² These results demonstrate that mirror neurons code the intention associated with the observed action. It appears that while observing other individuals achieving their own intentions, the primate's brain simulates those actions and intentions as if the observer were personally achieving those actions.

Another important property of mirror neurons has been discovered recently. Grasping execution cells in

the ventral aspect of F5c fire during observation of tool use actions.²³ Early studies on mirror neurons had demonstrated that mirror neurons do not fire during tool use actions. This made sense because monkeys do not use tools. The recently discovered tool-use mirror neurons likely represent acquired visual properties in mirror neurons because of visual experience (ie, the repeated exposure to human experimenters using tools and testing tool-use properties in mirror neurons during experimental sessions). The acquired tool-use properties of mirror neurons suggest that these neurons are shaped by visual experience, and thus may be critical for imitative learning.

Human Imitation and Mirror Neuron Areas

A transcranial magnetic stimulation (TMS) study provided the earliest evidence for mirroring mechanisms in the human brain. While observing grasping actions, subjects had higher motor excitability compared with control conditions.²⁴ Early positron emission tomography studies on the human mirror neuron system also adopted grasping observation (and execution) paradigms and provided initial evidence for human mirror neuron areas in inferior frontal and inferior parietal cortex.^{25,26}

Functional magnetic resonance imaging (fMRI) was used to test whether human areas relevant to imitation of hand actions had mirror properties. It was indeed found that inferior frontal and rostral posterior parietal areas had greater signal increases during action execution than action observation, a pattern similar to the discharge of mirror neurons in macaques. Furthermore, the signal increase in inferior frontal and rostral posterior parietal areas during imitation was approximately the sum of the signal increases during action execution and action observation. This made sense because imitation entailed both observation of the action and its immediate execution.²⁷ Further fMRI studies on imitation of hand actions demonstrated that the inferior frontal mirror neuron area is especially concerned with the goal of the imitated actions,²⁸ and with forms of imitation particularly dominant early on in life.²⁹ When imitating face-to-face, young children imitate almost exclusively as if in front of a mirror.³⁰ Mirror neuron areas in adults show the highest activity during this form of imitation.²⁹

When repetitive TMS was applied over the pars opercularis of the inferior frontal gyrus, a deficit in imitative behavior was demonstrated.³¹ This TMS study shows a causal relation between the inferior frontal mirror neuron area and imitative behavior, a relation that was not fully demonstrated by previous brain imaging experiments.

Imitation is a pervasive form of learning in humans, and the understanding of its underlying neural mechanisms is obviously important. A recent fMRI study demonstrated that the human mirror neuron system is

critically involved in imitative learning through neural interactions with motor preparation areas and dorsolateral prefrontal cortex.³² In keeping with these results, fMRI studies have demonstrated higher responses in mirror neuron areas during observation of overlearned actions.^{33,34}

Social Cognition and Mirror Neuron Areas

An influential model of how we understand the mental states of other people has suggested that we mentally put ourselves in other people's shoes, simulating what others do, feel, and think.³⁵ The properties of mirror neurons obviously map well on this framework.³⁶ Evidence in support of the idea that human mirror neuron areas implement a simulation-based form of understanding other people's mental states is provided by several imaging studies.

In a recent fMRI study, subjects watched grasping actions embedded in two different contexts, one suggesting that the intention of the grasping action was drinking, and the other one suggesting that the intention was cleaning up. Subjects also watched grasping actions with no context and contexts (scenes with teapot, cookies, a cup, and so on) without any grasping action. It was found that the inferior frontal mirror neuron area coded differently grasping actions with and without contexts, and it also responded differently to the same grasping action embedded in two contexts (Fig 2). These results cannot be readily explained by the account that mirror neuron areas code the action itself, but they can be easily accounted for by assuming that human mirror neuron areas code the intention associated with the observed action.³⁷

A fundamental aspect of social behavior is the ability to understand the emotional states of others and to empathize with them. Mirror neurons may provide a simulation-based form of empathy, possibly through interactions with more classic emotional brain areas, such as the limbic system. An fMRI study of observation and imitation of facial emotional expressions has demonstrated a large-scale neural network comprising mirror neuron areas, the anterior insula, and the amygdala.³⁸ These data are compatible with the hypothesis that mirror neurons help us in understanding and possibly feeling the emotions of others by simulating their facial expressions.

Evidence for a link between the human mirror neuron system and empathy also has been provided by three recent studies from three different laboratories. In one study, fMRI was used to measure activity in mirror neuron areas during observation of grasping actions. When activity in these areas was correlated with the subjects' tendency to empathize as measured by well-validated empathy scores, a robust correlation emerged.³⁹ In another fMRI study, subjects listened to action sounds. When subjects with high empathy

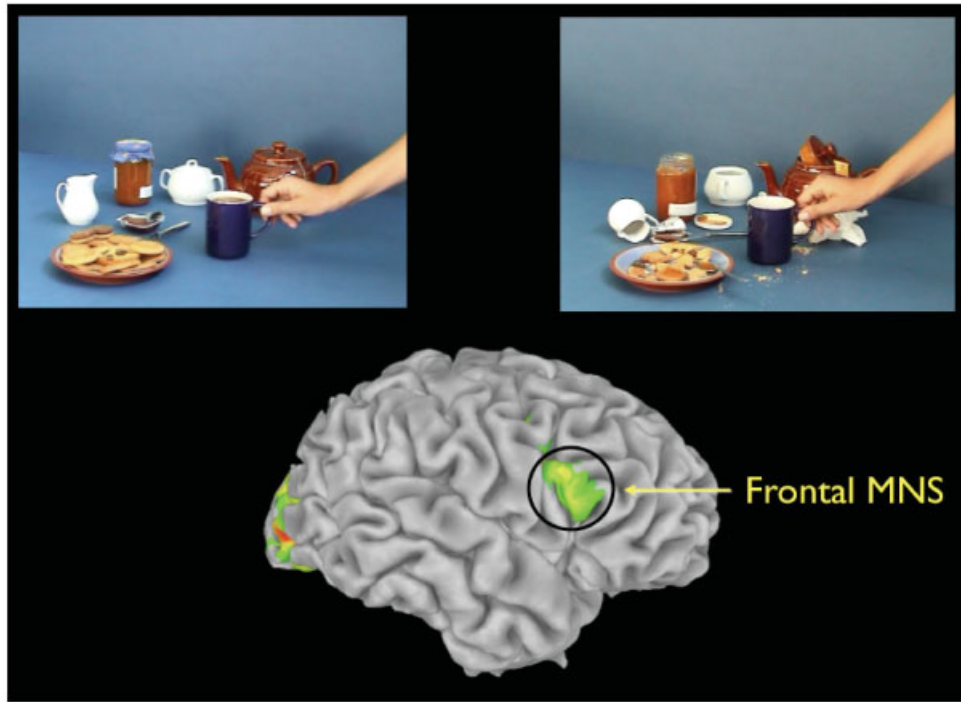


Fig 2. The right inferior frontal mirror neuron area codes differently the same grasping action embedded in two contexts, suggesting different intentions (drinking on the left and cleaning up on the right). This pattern of activity suggests that this area codes the intention associated with the observed action rather than the action itself. (Modified from Iacoboni and colleagues.³⁷)

scores were compared with subjects with low empathy scores, it was found that subjects with high empathy scores had greater activity in mirror neuron areas.⁴⁰ Finally, a TMS study measured motor excitability in subjects observing stimuli depicting pain inflicted to people. The changes in motor excitability correlated again with empathy scores of participants.⁴¹

Clinical Applications: Autism

The hypothesis that a core deficit of autism is the dysfunction of the mirror neuron system^{42–44} is appealing because it could account for three major symptoms of the disease: motor deficits, language impairment, and social impairment. Mirror neurons are, after all, just a special class of premotor neurons. A disorder in the mirror neuron system can conceivably account for the motor deficits of autism. There are also strong theoretical⁴⁵ and empirical⁴⁶ links between mirror neurons and language. A dysfunction of the mirror neuron system could account for the language disorders of autism. Finally, the links between the human mirror neuron system and social cognition reviewed in the previous section of this article suggest that a mirror neuron dysfunction could also account for the social deficits in autism.

Several laboratories, using a variety of techniques, have provided evidence for mirror neuron dysfunction in autism.^{47–51} A recent fMRI study of observation and imitation of facial emotional expressions has also

shown deficits in children with autism compared with typically developing children. Furthermore, this study has demonstrated robust correlations between the reduced activity in mirror neuron areas and the severity of the disease: the more reduced was the activity in mirror neuron areas, the greater was the impairment in subjects with autism.⁵²

The links between mirror neuron dysfunction and autism, and between mirror neuron system and imitation, have recently inspired intervention strategies based on imitation. Indeed, imitation deficits in autism are well documented and robust.^{53,54} Recent reports have provided preliminary evidence of a beneficial role of interventions based on imitation in children with autism.^{55–59} What is highly appealing of this approach is that some of these techniques can be easily taught to parents who can administer the intervention at home, with seemingly beneficial effects.⁵⁹

Clinical Applications: Motor Rehabilitation after Stroke

The activation of premotor neurons during simple observation of actions is a highly appealing feature for rehabilitation of motor functions. A chronic motor disorder is observed in a large number of patients who survived stroke.⁶⁰ The use of action observation as a form of rehabilitation is obviously highly appealing in patients with severe paresis for whom active rehabilita-

tion may be difficult.⁶¹ More generally, action observation as a form of training in rehabilitation has been recently proposed on theoretical grounds.⁶² The first empirical study supporting these ideas has been published recently.⁶³

In this study, two groups of stroke patients had the same physical training and additional “observation” sessions. The experimental group observed videos of everyday arm and hand actions, whereas the control group observed sequences of geometric symbols and letters. The experimental group demonstrated a significant improvement of motor functions compared with both pretreatment baseline and control groups. Furthermore, both groups of patients were studied with fMRI before and after treatment. The activation task used in this study, object manipulation, was a motor task ostensibly unrelated to the everyday actions shown in the videos to the experimental group. Whereas the control group demonstrated substantially no changes in brain activity during object manipulation before and after treatment, the experimental group demonstrated widespread increases in activity after treatment in mirror neuron areas and other cortical areas of motor significance. When these changes were formally compared between the two groups, significant increases in activity were observed again in inferior frontal and inferior parietal mirror neuron areas, and in a small additional set of areas, the supplementary motor area, insula, and superior temporal gyrus.⁶³

Although this study is currently the only empirical study on the effect of action observation in rehabilitation, and future studies are definitely needed, its results are impressive and exciting.

Conclusion

The first preliminary report on mirror neurons was published 15 years ago.¹³ In the relatively short time since that publication, we have largely improved our understanding of this neural system, and were able to successfully translate basic concepts to initial clinical applications in both psychiatry and neurology.

The future work on the mirror neuron system should consolidate and expand the clinical applications whereas also filling the gaps in the basic science. After all, mirror neurons have been studied only with single-cell recordings in macaques and with a variety of brain imaging techniques in humans. It is important to obtain brain imaging data in monkeys⁶⁴ and single-unit recordings in humans to fill the gap.⁶⁵ Some of these studies are already available^{64,65} and others will certainly follow.

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