Mirror Neurons
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The term mirror neurons originally referred to neurons in the ventral premotor cortex of macaque monkeys (area F5, Figure 1a) that have the particularity of responding both when the monkey performs a particular action (e.g., grasping a peanut) and when the monkey perceives another individual performing a similar action. More recently the term mirror has been extended to areas of the human brain that have similar properties. Mirror neurons may explain a large number of social cognitive functions, including the understanding and imitation of the actions of others, empathy, and language. This entry reviews the core findings on mirror neurons in monkeys and discusses their functional significance. I will also review evidence for a similar system in humans and discuss the specific role of this system in humans.

Mirror Neurons in the Monkey

Mirror neurons are found in the rostral part of the ventral premotor cortex of monkeys. I will first describe the motor properties of neurons in this part of the cortex and then discuss the sensory properties of those neurons in area F5 that are called mirror neurons.

Motor Properties of F5 Neurons

Neurons in area F5 of the monkey (Figure 1a) respond when the monkey performs a goal-directed action. Goal-directed actions are those in which an effector (fingers or mouth) interacts with an object. Examples of goal-directed actions during which F5 neurons are active are grasping, holding, tearing, and breaking objects with the hand or mouth. The discharge of F5 neurons during the execution of these actions occur even if the eyes of the monkey are closed and are therefore thought to be involved in the motor execution of the action. F5 neurons do not respond when the monkey performs movements not directed at a goal, such as simply moving the
arm or fingers. The area has therefore been considered to be involved in the preparation of goal-directed movements and to be part of the motor system of the monkey.

Individual F5 neurons respond selectively during the execution of one of the aforementioned actions. Some neurons respond when an object is grasped between the index and the thumb (precision grip), others when then monkey grasps an object using the entire hand (whole hand prehension), others still when the monkey grasps an object with both hands and breaks it (Figure 1b), and so on. The narrowness of the motor selectivity of the neurons varies: some fire vigorously during precision grip and remain silent during whole hand prehension; however, most neurons respond to both actions, but with significantly more firing for one or the other.

In contrast to the primary motor cortex, where the movements of particular muscle groups are represented, F5 codes actions at a higher level of abstraction. F5 grasping neurons usually respond whether the monkey grasps an object with the right or left hand. They often respond even when the grasping is done with the monkey’s lips and teeth. All these instances involve different effectors but have the grasping in common. The neurons therefore represent the action (grasping) and not the precise movements involved. F5 neurons have therefore been considered to build a ‘vocabulary’ that can be used (like the words of a phrase) to build complex action sequences, without going into the details of what muscles will be used to perform the action. Activity in a given neuron would then be equivalent to the order ‘precision-grasp it!’; activity in another ‘break it!’; and so on. Depending on the environmental situation, the output from such a neuron must then be transformed into a more detailed sequence of muscle contractions.

**Mirror Neurons and the Sensory Properties of the Premotor Cortex**

Although the aforementioned motor properties of F5 have been known for a while, more recently the research group around Rizzolatti, Gallese and Fogassi made an odd observation. They recorded in F5 to determine what actions were best at driving a particular neuron when performed by the monkey (‘best motor action’). Accidentally, they observed that some of these neurons also responded when the experimenter happened to perform a similar action in front of the monkey. They then performed a number of systematic studies that confirmed this observation and showed that some of the neurons in F5, particularly those in the convexity close to the arcuate sulcus, responded not only when the monkey performed an action (Figure 1b) but also when he observed someone else (human or monkey) perform a similar action (Figure 1c). Other, dissimilar actions were much less effective at causing a response in these neurons, whether they were observed or executed by the monkey. These neurons were coined ‘mirror neurons.’ Given that the neurons are located in the motor cortex of the monkey, most people never attempted to characterize the response of these neurons in visual terms, which is why they remained undiscovered for such a long time.

Why this term mirror neurons? The observation of an actor’s (the term actor here is used to refer to a person or monkey that does an action in front of an observer) actions activated neurons in the brain of the observer (the term observer is used in this article to refer to a human or monkey that is looking at and listening to what someone else is doing, so our observer is both an observer and a listener; the same is true for any form of the verb to observe, which will mean both looking and listening) that are normally activated when this observer performs the actions himself. This means that the observer internally simulated the observed actions, as if he were making them himself. These neurons are therefore called mirror neurons, because the activity in the mirror neurons of the observer resembles that in the brain of the actor – the neurons thus mirror the activity in the actor’s brain, much like a mirror reflects a pattern of light that is similar to that reflected by the person in front of it.

Mirror neurons have so far been found for all the actions typical for F5 neurons: grasping, breaking, tearing, biting, and holding objects with the hands and mouth. Mirror neurons preferred the same actions when performed and observed. This congruence in the visual and motor selectivity of the neurons is essential for the functional significance of these neurons. Their selectivity in turn is typically graded: a neuron that prefers breaking will also, but to a much lesser extend, respond during the forceful grasping of an object, while remaining silent when you simply wave your arm around. Taking a population of such graded neurons, some preferring grasping, others breaking, etc., creates a population activity that unambiguously describes a particular action.

Most recently, we could show that some mirror neurons additionally have the capacity to respond to their preferred action, even if the monkey only hears the sound that is normally associated with the action. Figure 1d illustrates the responses of such a neuron. This is the same mirror neuron shown in
Figures 1b and c, but this time the monkey only hears someone else break a peanut. Not all mirror neurons respond to the sound of action; the subclass that does is called audiovisual mirror neurons. Clearly, audiovisual mirror neurons are only found for actions that have characteristic sounds, such as breaking or tearing, and not for simple grasping, which is silent.

Figure 2 (and Movie 1) illustrates two additional important properties of mirror neurons. The exemplified mirror neuron responds when the monkey grasps an object and is therefore a grasping mirror-neuron. The same neuron responds vigorously when the experimenter grasps an object in full sight of the monkey (Figure 2a). The same grasping movement mimed out without the presence of the object causes much less response (Figure 2c). Virtually all mirror neurons display this behavior: they respond only if the action is directed at an object. They therefore respond to the action of grasping and not simply the hand movements involved in grasping. Figures 2b and d illustrate a behavior observed in about half of the mirror neurons: if an occluding screen is slid in front of the object and the experimenter grasps the object behind the screen (b), the mirror neuron responds as if the monkey had seen through the opaque occluding screen. If, on the other hand, the occluding screen is closed after the monkey has seen that there is no object to be grasped behind it,
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**Movie 1** Mirror neurons and occluded actions. The movie shows the monkey’s perspective on the four conditions illustrated in Figure 2, whereas the audio track represents the response of the mirror neuron of Figure 2 when the monkey observes the stimuli. Note that the neuron responds when the experimenter grasps the orange – whether or not it is in sight – and that it responds much less if the experimenter pretends to grasp when no orange is present.

no discharge occurs (d). This demonstrates the capacity of the mirror neurons to make a meaningful completion of visual stimuli based on what the animal saw in the past (orange present/absent). Mirror neurons are therefore not only motor, visual, and auditory neurons—they can also represent mental contents such as the ‘knowledge’ of whether an orange is present or not.

Finally, it appears that F5 is not the only brain area that contains mirror neurons. Mirror neurons have also been found in the rostral inferior parietal lobule (area PF/PFG). This suggests that the visual information travels to F5 through the parietal area PF/PFG, which is heavily interconnected with F5.

**Functional Significance of Mirror Neurons in Monkeys**

The discovery of mirror neurons has a fundamental impact on many issues. I will outline some of the implications below.

**Mirror neurons and the ‘idea’ of actions** The fact that mirror neurons respond to an action when it is performed, seen, or heard suggests that these neurons represent the preferred action at a remarkable level of abstraction. There is nothing in common between the sight of an action and the sound of this action, except for the abstract concept of the action. Mirror neurons seem to represent this abstract concept when the monkey performs the action (whether it is performed with one hand or the other, or often even with the mouth) or when the monkey observes the actions (whether heard or seen). This high level of abstraction is observed in monkeys. If a human says that his actions are fundamentally the same as the actions of someone else, we would consider this a sophisticated abstract thought. The fact that mirror neurons respond in similar ways to the monkey’s own actions and those of another suggest that primes might possess a remarkable form of proto-semantics. It is interesting that this abstraction occurs in an area that has been classically considered to be rather pragmatic – the premotor cortex. A stimulating hypothesis is therefore that abstract thinking may derive from the skilled machinery of perception and action. Thinking would then be a form of inner motor action.

**Mirror neurons and the recognition of actions** Although a comprehensive understanding of the function of mirror neurons in the monkey brain is still lacking, one of the most plausible hypotheses is that these neurons could contribute to the ability to recognize the actions of others. Recognizing actions is a challenging task. At a visual level, there is very little in common between seeing an actor break a peanut with his teeth and seeing him break a peanut between his two hands, yet mirror neurons respond in both cases as if they had recognized that in both cases the actor broke the peanut. The same neuron responds even if the monkey only hears the actor break the peanut. The mirror neurons seem to have the capacity to selectively respond to very diverse instances of breaking, while remaining silent if a hand performs a very similar movement without interacting with an object (Figure 2c). How can the neurons find out what is breaking and what is not? The following scenario might give us an answer. When we observe ourselves perform an action, we know what we are trying to do, see what movements our hands are performing, hear the auditory consequences of the action, and feel the rewarding touch of the object in our hand. Goals, motivations, and the sight and sound of our own actions therefore synchronize in time with the activity of the premotor neurons that command the action – a condition known to be ideal for associative ‘hebbian’ learning. At the neural level, this learning during self observation is thought to strengthen the synaptic connections between (a) the premotor neurons commanding the action and (b) the different visual and auditory neurons activated by the observation of our own action. When we then see someone else perform the action, the sound of the action is very similar to the sound when we make the same action, and the sight of the other person’s hands making the action is similar to that of our own hands making the action (although seen from a somewhat different perspective). This sensory input is then able to activate the premotor neurons representing the same action through the strengthened synaptic connections selected during the hebbian learning. The activation of this network then becomes indicative of the action...
independently of who performs it and how it is perceived and represents a form of classification or recognition of the action. This recognition can occur even when we only hear the action or only partially see the action.

Indeed, we recently demonstrated that the activity of mirror neurons can be used to tell which of two actions had been performed in front of the monkey with a near-to-perfect accuracy, supporting the idea that mirror neurons could very well be used to recognize actions.

**Sensation and action** Classically, sensation, or the process of perceiving what happens around us, has been conceptualized as something fundamentally different and separate from action. The exploration of brain function has therefore been split into different camps, each claiming particular brain areas. The camp of the visual neuroscientists claimed areas such as V1, V2, V3, V4, and IT. Motor neuroscientists claimed brain areas such as M1, premotor cortex, supplementary motor cortex, etc. In the areas claimed by the visual neuroscientists, responses are recorded while visual stimuli are presented to the monkey. At the same time, in areas claimed by the motor neuroscientists, responses are investigated while the monkey performs actions. The discovery of mirror neurons has shown us that this approach is mistaken, and slows down our understanding of the brain: neurons that are both visual and motor have long been thought to be purely motor, and this belief was not falsified because, being thought to be motor neurons, they were not tested with visual stimuli. We should hence revise our vision of the brain and accept that it is a machine to transform sensation into action. For this aim, substantial sectors of the brain will have mixed sensory and motor properties.

This mixed architecture helps us transform a visual stimulus in the appropriate motor response, but it also means that our motor expertise might help us understand visual stimuli. The response of mirror neurons when part of an action is occluded illustrates this possibility. The monkey’s motor schemata code that grasping an orange is what you do when you are hungry and see an orange. Hence, when seeing someone reach behind an occluding screen with an orange behind this occluder, mirror neurons may respond as if they saw that the orange was grasped, because these same neurons are part of a network that would make the monkey himself grasp the orange behind this same occluder. Our understanding of the world may thus derive in part from our own actions.

**Mirror neurons and social cognition** For social species like humans and monkeys, success depends to a large extent on how good one is at understanding the inner life of others. Important questions for humans include examples such as these: Is my boss angry at me? Does my girlfriend look at this man because she is falling in love with him? Similarly, monkeys question the inner life of other monkeys: Is the dominant monkey over there hungry, or can I eat his peanuts without getting beaten up? Assigning goals and motivations to others is called mind reading, and in the absence of telepathy, mind reading must be based on the observation of the behavior of others. Mirror neurons may be a key to this behaviorist mind-reading: When we perform an action, in addition to associating the sight, sound, and execution of an action, we also synchronize the execution of the action with the ideas and motivations that led us to make this action. We break peanuts when we are hungry but not when we are thirsty. When we see someone else breaking a peanut, this will therefore activate not only our own premotor representation of peanut breaking but possibly also the network of motivation such as hunger, which is usually active when we break peanuts. Through this network, we can then retrieve the representations of goals and motivations of others and attribute those representations to the observed acting individual. This simple mechanism then gives us an intuitive but profound understanding of the action: He is breaking a peanut because he is hungry and wants to eat it – so I better not take those peanuts. In a way, we ‘empathize’ (the term empathize is used in a somewhat unconventional sense in this context: it means to share goals and motivations with an actor, without necessarily involving emotions) with the observed actor, and we may even feel hungry ourselves. Mirror neurons would then be a simple mechanism, trained through hebbian learning, that enables an observer to understand the actions of others as if the observer were doing these actions himself or herself. We mentally put ourselves ‘in the shoes of the other’ – a type of mind reading referred to as the simulation theory. The concept that mirror neurons are part of a network that uses our own actions to mind-read other people or other monkeys has an interesting implication: the brain implicitly assumes that others are fundamentally similar to ourselves – if I break peanuts when I am hungry, and he broke a peanut, then he must be hungry too.

Another fascinating aspect about the idea of empathy being a simulation is that it makes empathy a very intuitive process, the result of hebbian association between actions and motivations rather
than a complex cognitive process that might be expressed as, ‘Let’s see... he broke a peanut, so what could he feel?’ The fact that monkeys have mirror neurons may indicate that they already have such an intuitive capacity to empathize.

In few words: mirror neurons make the social world predictable by giving us insights into what others do and why they do it.

It is important to note that although the idea that mirror neurons may be the key to many social cognitions is stimulating, it is also highly speculative. Much work is needed to test this theory.

**Mirror neurons and imitation** It is intuitively appealing to assume that the activity of mirror neurons may reflect the tendency to imitate the actions of others. Could the activity that occurs in the premotor cortex when one monkey sees another perform a similar action simply be due to the fact that the observing monkey imitates the action he observes? The activity of mirror neurons would then reflect ‘true’ motor activity. Behavioral and electrophysiologic evidence falsifies this hypothesis. First, electromyographic recordings of the hand muscles of monkeys show that grasping mirror neurons can become activated even if the observing monkey does not activate his hand muscles. Second, monkeys do not display true imitative behavior: shown how to open a complex box containing food, monkeys will not then attempt to open the box in the way they just observed. Imitation, therefore, cannot explain the mirror activity observed in the monkey’s brain.

**The Mirror System in Humans**

Since the discovery of mirror neurons in the monkey, several imaging experiments have demonstrated that there are brain areas in humans that are activated both when a human subject makes particular actions (Figure 3, top) and when he or she observes someone else perform similar actions (Figure 3, bottom). In the frontal cortex, the opercular part of the inferior frontal gyrus constitutes the ventral premotor cortex (~area BA44) and is bilaterally activated both by the execution and the observation of hand actions such as object grasping and manipulation. The same is true in the anterior part of the interparietal sulcus (~BA40) of the parietal cortex. These two brain areas are therefore thought to create a frontoparietal mirror system in humans.

![Figure 3](image)

**Figure 3** The human mirror system. Cortical activation pattern overlaid on lateral views of the human cortex, measured using fMRI while subjects manipulated an object (top, adapted from Binkofski F, Buccino G, Posse S, et al. (1999) A fronto-parietal circuit for object manipulation in man: evidence from an fMRI study. European Journal of Neuroscience 11: 3276–3286) and observed another individual grasping an object (bottom, adapted from Buccino G, Binkofski F, Fink GR, et al. (2001) Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. European Journal of Neuroscience 13: 400–404). Note how the frontal and parietal activations overlap in the two conditions. In the bottom row, significant activation in the visual cortex is shown in gray to differentiate it from the parietal and frontal activity common to both conditions.
Humans. Clearly, brain imaging can demonstrate only that a given area is activated in both conditions—not whether the same neurons are active under both conditions. We should therefore speak of mirror areas. In the light of the single neuron evidence in monkeys, it is likely that the activity of mirror areas during execution and observation derives from the activity of mirror neurons in these areas.

Initially, the discovery of a representation of hand actions in area BA44 was controversial. BA44 constitutes the caudal part of Broca’s area. Lesions in Broca’s area cause speech production deficits, and BA44 was therefore thought to be exclusively responsible for the execution of the orolaryngeal movements necessary for speech. The aforementioned experiments changed this view, and BA44 is now also considered responsible for hand and finger movements. BA45, a more anterior aspect of Broca’s area, on the other hand, is activated during more semantic tasks such as the naming of observed actions or the verbalization of objects that are grasped. BA45 is therefore considered to be a more strictly verbal and semantic sector of Broca’s area.

Indeed, the frontoparietal mirror system in humans seems to map the body of the actor onto that of the observer, with observed mouth actions activating more ventral sectors than observed foot actions, in agreement with Penfield’s classic description of the somatotopic organization of the motor cortices.

Although it is always difficult to establish homologies between brain areas in different species, BA44 is thought to be the human homolog of the monkey’s area F5, which also responds during both hand and mouth actions. The existence of mirror neurons in the monkey’s F5 therefore supports the idea that the mirror activity of the brain area BA44 in humans is due to the activity of mirror neurons in this area.

Independent evidence for the existence of a mirror system in humans stems from a transcranial magnetic stimulation (TMS) experiment. These demonstrate that showing a movie of a particular hand movement facilitates the execution of that hand movement in the observing individual. Such facilitation is suggestive of the fact that neurons responsible for the execution of these movements receive visual input about the sight of the same action—the very connection that is characteristic for mirror neurons.

Finally, there is evidence suggesting that the mirror system may apply beyond the realm of motor actions. Hutchison recorded from single neurons in the human brain that were sensitive to the feeling of pain: the neuron responded if the finger of the patient was stuck with a needle. The same neuron also responded while the patient watched someone else being stuck by a needle. These neurons transformed the sight of someone else being stuck into the observer’s inner feeling of pain, creating a strong empathic bind between the actor and the observer.

**The Mirror System and Human Cognitive Capacities**

The implications of mirror neurons discussed for monkeys also apply to humans. In addition, humans, unlike monkeys, can imitate actions. It is likely that mirror neurons, although serving a different function in monkeys, may have been an important building block in the evolution of imitation. Indeed the frontoparietal mirror system becomes particularly active when a subject needs to imitate finger movements he is observing on a screen.

In addition, the fact that mirror neurons in monkeys have been found in area F5, which is thought to be the homolog of area BA44 of the human speech production area, supports the idea that hand gestures and the mirror system may have played a seminal role in the evolution of language. This idea receives additional support from our recent discovery that even in the monkey, the mirror system receives input from the auditory modality so characteristic of human speech and is able to discriminate between different sounds.

**See also:** Motoneurons; Motor Cortex; Oscillatory Responses of the Brain and Cognitive Correlates; Response Synchronization in the Visual Cortex; Social Cognition; Visual Perception.

**Further Reading**


