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Mirror Neurons and Mirror Systems in Monkeys and Humans

Maddalena Fabbri-Destro^{1,2} and Giacomo Rizzolatti¹

¹Dipartimento di Neuroscienze, Sezione Fisiologia, Università di Parma, Parma; and ²Dipartimento SBTA, Sezione di Fisiologia Umana, Università di Ferrara, Ferrara, Italy
giacomo.rizzolatti@unipr.it

Mirror neurons are a distinct class of neurons that transform specific sensory information into a motor format. Mirror neurons have been originally discovered in the premotor and parietal cortex of the monkey. Subsequent neurophysiological (TMS, EEG, MEG) and brain imaging studies have shown that a mirror mechanism is also present in humans. According to its anatomical locations, mirror mechanism plays a role in action and intention understanding, imitation, speech, and emotion feeling.

Mirror neurons are a class of neurons that become active both when individuals perform a specific motor act and when they observe a similar act done by others. In primates, mirror neurons have been found in the premotor cortex and in the inferior parietal lobule (22, 20, 51). Recently, mirror neurons also have been described in the forebrain of birds (48).

The essence of the mirror neuron mechanism is the transformation of specific sensory information into a motor format. This mechanism can be demonstrated, besides recording single neurons, by using transcranial magnetic stimulation (TMS), EEG, MEG, and brain imaging technique (PET, fMRI). Evidence of the existence of mirror mechanism in humans is based on these techniques.

The functions mediated by the mirror mechanism vary according to its location in the brain networks. Among the networks endowed with a mirror mechanism (mirror systems), the most studied is the one formed by the inferior parietal lobule and the ventral premotor cortex. This network transforms sensory representations of observed or heard motor acts into motor representations of the same acts. Its function is to give an immediate, not cognitively mediated, understanding of the observed motor behavior. A mirror mechanism is also present in the insula and rostral cingulate (16, 23). This mechanism transforms observed emotional situations into visceromotor responses analogous to those that are present when an individual actually experiences those emotions. This emotional mirror system gives the observer a direct feeling of what others feel. Other networks containing a mirror mechanism are involved in coding intransitive movements and in transforming heard phonemes in motor acts able to generate them.

In this review, we will examine first the mirror mechanism involved in action and intention understanding. We will review then mirror system involved in coding non-object-directed movements (i.e., intransitive movements) and verbal material. We will conclude with discussing mirroring and emotion.

Mirror Neurons and Action Understanding

The parieto-frontal mirror system in the monkey

Mirror neurons have been first discovered in a sector of the ventral premotor cortex (area F5) of the monkey (22, 51). Subsequently, they have been also found in the inferior parietal lobule (20). The defining characteristics of parietal and premotor mirror neurons is the close relationship they show between the motor acts they code and the visual motor acts they respond to (FIGURE 1). Using as classification criterion the congruence between the executed and observed motor acts effective in triggering them, the mirror neurons have been subdivided into two main classes: strictly congruent and broadly congruent mirror neurons. Strictly congruent mirror neurons discharge when the observed and executed effective motor acts are identical both in terms of goal (e.g., grasping) and in terms of the way in which that goal is achieved (e.g., precision grip), whereas broadly congruent mirror neurons require, to be triggered, similarity but not identity between the observed and executed effective motor acts (22).

FIGURE 2 shows the cytoarchitectonic organization of the parietal and agranular frontal cortices of the monkey. Area F5 represents its frontal node (53). This area is not homogeneous. Cytoarchitectonically, it consists of three sectors: a sector lying on the cortical convexity (F5c), a sector located on the dorsal part of the posterior bank of the arcuate sulcus (F5p), and a sector located on the ventral part of the same bank (F5a) (38) (FIGURE 2, LEFT INSET).

Mirror neurons are located mostly in F5c. In F5p, a different type of visuo-motoneurons have been described. These neurons, called “canonical neurons,” respond to the presentation of 3D objects but do not require an action on them to be activated (38).

There are no single neuron data on the functional properties of F5a. A recent fMRI study revealed, however, an interesting functional difference between this

area, on one side, and F5c on the other. This study showed that, although to be activated F5c requires an “embodied” situation, which is the vision of the agent performing the motor act, the more rostral F5a codes motor acts in a more abstract way, becoming active even when the acting hand only is visible (41).

How does visual information reach area F5? Recently, an experiment in which fMRI data were combined with anatomical tracing techniques showed that there are two main anatomical and functional streams that, via inferior parietal lobule, connect area F5 with the higher order visual areas of the superior temporal sulcus (STS). The first stream originates from a sector of the upper bank of the STS (“STPm”), reaches parietal area PFG, and terminates in area F5c. The second stream arises in the lower bank of the STS, reaches parietal area AIP, and then area F5a (3, 42). Studies of Perrett and coworkers showed that neurons of STS region respond to the observation of motor acts

performed by living individuals (32, 46). STS, however, should not be properly considered as a part of the mirror neuron system because its neurons do not discharge in association with motor activity.

Before examining what might be the functional role of the mirror neurons, it is important to define some terms at the basis of motor organization: movement, motor act, and action. Movement indicates a mere displacement of a body part. It does not include the idea of goal. Motor act defines a series of movements performed to reach a goal (e.g., grasping an object). Finally, motor action is a series of motor acts (e.g., reaching, grasping, bringing to the mouth) that allows individuals to fulfill their intention (e.g., eating).

The most widely accepted hypothesis on the functional role of the parieto-frontal mirror circuit is that it plays a role in understanding the goal of motor acts, which is what an individual is doing in a given moment (e.g., grasping, holding, tearing) (52). To test this

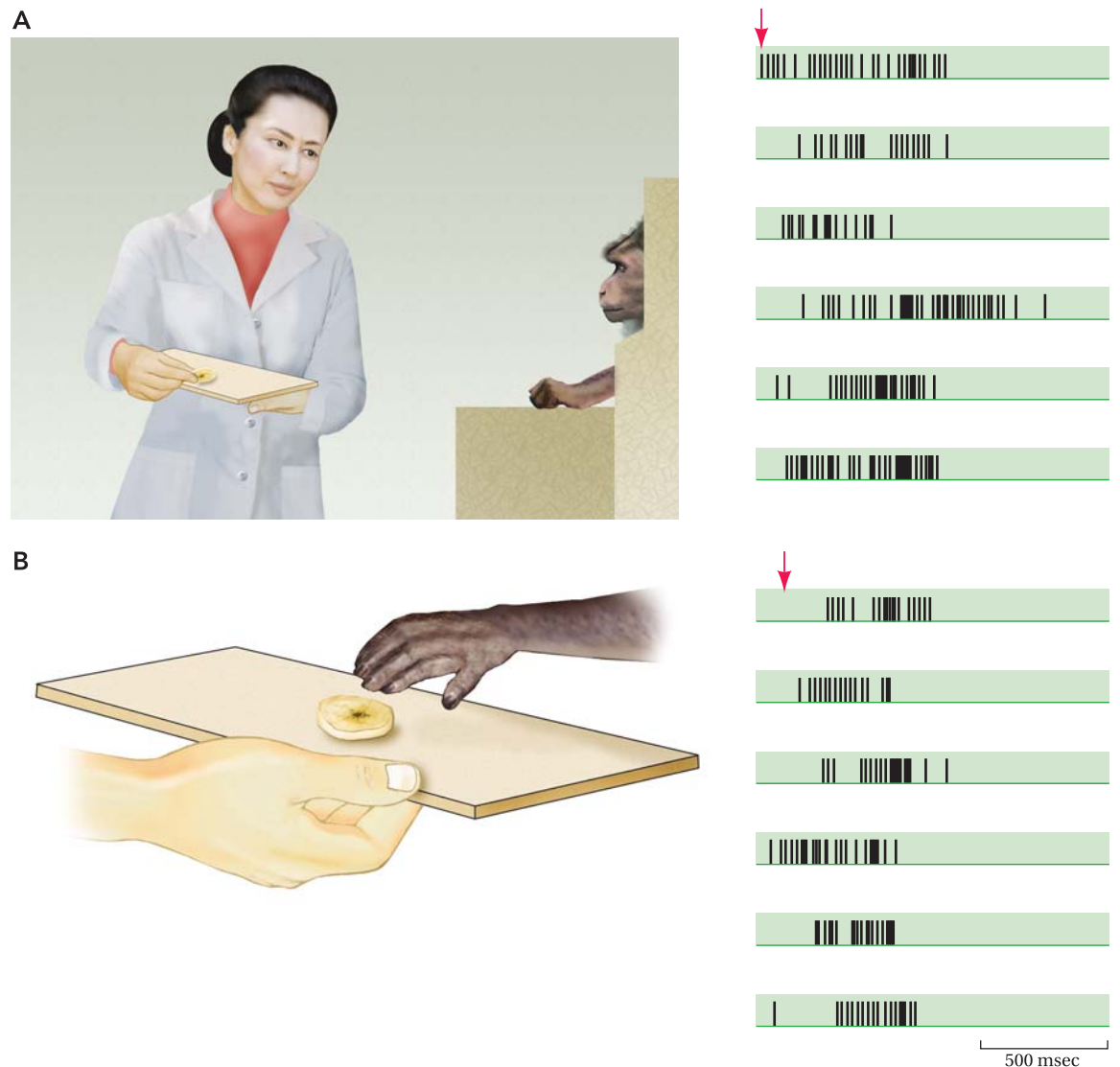


FIGURE 1. Example of a F5 mirror neuron
The neuron discharges during observation of a grasping movement done by the experimenter (A) and during monkey grasping movements (B).

hypothesis, two series of experiments were carried out. In the first, the authors tested whether mirror neurons could recognize actions from their sounds. It was found that many mirror neurons that responded to visual observation of motor acts accompanied by sounds also responded to the sound alone. These neurons were named “audio-visual” mirror neurons (33). In the second series of experiments, after selecting mirror neurons that responded exclusively during the observation of the late phase of grasping and/or during object holding, these neurons were tested in two conditions. In one, the monkey saw the hand of the experimenter grasping and holding an object (“full vision” condition); in the other, the monkey saw only the experimenter’s hand moving toward a screen but not the final critical part of the motor act, i.e., the hand object interaction (“hidden” condition). The results showed that more than half of the F5 mirror neurons discharged in the hidden condition. This shows that when the monkey has sufficient clues to create a mental representation of the observed motor act, mirror neurons describe it even if the motor act is not visible (63).

Taken together, these experiments strongly support the notion that the activity of mirror neurons underpins the understanding of motor acts. This is regardless of whether this comprehension is based on vision, sound, or mental representation.

Although single mirror neurons code the motor act that is going on in front of the observer, there is recent evidence that, thanks to the functional organization of the parietal and premotor mirror neurons, the observer is also able to understand why that motor act is done, in other terms, the goal of the action of which motor act is part.

This evidence has been reached in one experiment in which monkeys were trained to perform two actions with different goals (20). In the first, the monkey had to grasp an object to place it into a 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, whereas 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 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 was followed by a subsequent specific motor act (e.g., placing).

Some of these action-constrained motoneurons 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) (20). Thus the activation of IPL action-constrained mirror neurons coded not only grasping but grasping for eating or grasping for placing. This specificity can allow 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: i.e., to understand the intentions behind the action’s agent.

Mirror system in humans

The human parieto-frontal mirror system mediates the same functions that are mediated by the homologous mirror system in the monkey: understanding the goal of actions done by others and the intentions behind them.

As shown by many brain imaging studies, the two main nodes of human mirror system are the inferior parietal lobule (IPL) and the ventral premotor cortex (PMv) plus the caudal part of the inferior frontal gyrus (IFG). This part roughly corresponds to the pars opercularis of this gyrus. The localization of human parieto-frontal mirror system is shown in FIGURE 3. As one can see, it closely corresponds to that of the homologous mirror neuron system of the monkey.

The premotor node of mirror system is somatotopically organized (4). Observation of motor acts done with different effectors determines activation of specific parts of it. Leg, hand, and mouth movements are

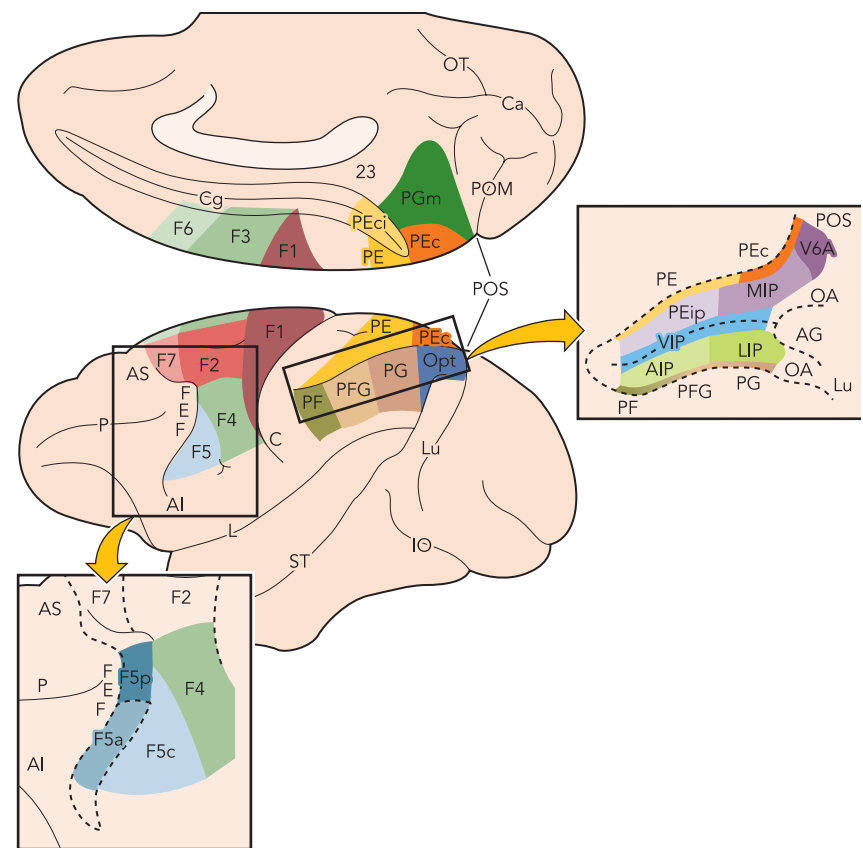


FIGURE 2. Mesial and lateral views of the macaque brain
 The central part of the figure shows the cytoarchitectonic parcellation of the frontal motor cortex (areas indicated with F and Arabic numbers) and of the parietal lobe (areas indicated with P and progressive letters). The enlargement of the frontal region (rectangle on the left) shows the parcellation of F5. The rectangle on the right shows the areas buried within the intraparietal sulcus. AIP, anterior intraparietal area; IP, intra-parietal sulcus; LIP, lateral intraparietal area; MIP, medial intraparietal area; POS, parieto-occipital sulcus; AS, superior arcuate sulcus; AI, inferior arcuate sulcus; C, central sulcus; Ca, calcarine fissure; CG, cingulate cortex; FEF, frontal eye field; L, lateral sulcus; Lu, lunette sulcus; P, principal sulcus; STS, superior temporal sulcus.

represented in a medial to lateral direction, as in the classical homunculus of Penfield and Woolsey (44, 68).

To shed light on the organization of cortical areas forming the action observation circuit, a study was recently carried out using four motor acts performed with the mouth, the hand, and the foot (31). In agreement with previous studies (43, 55, 65), the results showed that the ventral premotor cortex clusters together motor acts performed by the same effector, regardless of their positive (directed toward the agent) or negative (directed away from the agent) valence. In contrast, the parietal mirror node appears to follow another organization principle. Here, the various observed motor acts are coded not according to the effector performing them but according to the valence of the observed motor act. Positive motor acts activate ventral sectors of the responsive region (mostly phAIP), whereas negative acts activate dorsal sectors of the same area and the adjacent dorso-rostro-lateral cortex (31).

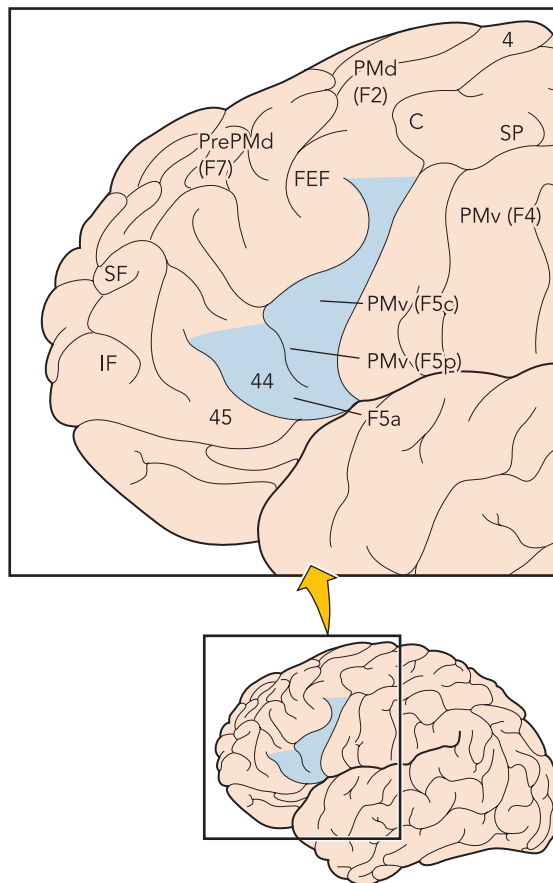


FIGURE 3. Later view of human cortex with an enlarged view the frontal lobe

Cytoarchitectonic subdivision according to Brodmann. The areas in yellow show areas responding to the observation and execution of hand motor acts. Top: enlarged view of the frontal lobe. The possible homology between monkey and human premotor cortex are indicated. C, central sulcus; IF, inferior frontal sulcus; FEF, frontal eye field; PMd, dorsal premotor cortex; PMv, ventral premotor cortex; PrePMd, predorsal premotor cortex; SP, upper part of the superior precentral sulcus. For areas indicated with F, see **FIGURE 2**.

Motor acts that are richly represented in the observer's motor repertoire determine a strong activation of the mirror system. This has been shown by a series of brain imaging studies that examined the mirror activations in persons expert in specific motor skills and comparing them with the activations determined by the same stimuli in individuals having different motor experience. The results showed that the observed actions are mapped onto the observers' corresponding motor programs and that the activation is stronger in individuals expert in performing them (8, 9, 12).

An issue that has been recently addressed is how the mirror system would respond to the observation of hand actions if the observer never had hands or arms (25). Two aplasic individuals, born without arms and hands, were scanned while they observed hand actions. The results showed activations in the parieto-frontal circuit while they were watching hand actions. This finding demonstrates the brain mirrors actions that deviate from normal motor organization by recruiting motor representations involved in the execution of actions that achieve corresponding goals using different effectors.

Convincing evidence has been recently achieved that, as in the monkey, the human mirror system also is involved in understanding not only the goal of the observed motor acts but also the intention behind them.

The first evidence in this sense has been provided by an fMRI study in which volunteers had to infer the agents' intention by observing them performing a motor act (30). In the study, there were three conditions. In the first condition (context), the volunteers saw some objects arranged as if a person was ready to drink the tea or had just finished the breakfast; in the second condition (action), the volunteers were shown a hand that grasped a mug without any context; in the third condition (intention), the volunteers saw the same hand action but within the two breakfast contexts. The contexts suggested the intention of the agent, i.e., grasping the cup for drinking or grasping it for cleaning the table.

The results showed that, in both action and intention conditions, there was an activation of the mirror system. Crucial was the comparison between intention and action conditions. This comparison showed that the understanding of the intention of the doer determines a significant increase in activity of the mirror system.

In conclusion, these data show that the intentions behind the actions of others can be recognized by the mirror mechanism. This does not exclude, of course, that other more cognitive ways of "reading minds" do exist (21). However, the mirror mechanism is most likely the most basic neural mechanism for a motor (experiential) understanding intentionality.

More recently, an fMRI study investigated the neural basis of human capacity to differentiate between actions reflecting the intention of the agent (intended

actions) and actions that did not reflect it (non-intended actions). Volunteers were presented with video clips showing a large number of actions done with different effectors, each in a double version: one in which the actor achieved the purpose of his or her action (e.g., pour the wine), the other in which the actor performed a similar action but failed to reach the goal of it because of a motor slip or a clumsy movement (e.g., spill the wine). The results showed that the observation of both types of actions activated a common set of areas including the inferior parietal lobule, the lateral premotor cortex, and mesial premotor areas. The contrast of non-intended vs. intended actions showed activation in the right temporo-parietal junction, left supra-marginal gyrus, and mesial prefrontal cortex. The converse contrast did not show any activation. The authors concluded that the capacity to recognize non-intended actions is based on the activation of areas signaling unexpected events in spatial and temporal domains, in addition to the activity of the mirror system (6). The interpretation of the right temporo-parietal junction activation as an attentional mechanism is in line with introspection that a non-intended action does not produce attempts to attribute an intention to the agent as well as with recent data stressing the role of this region in attentional processes (40).

Intransitive Actions and Imitation

The mirror system that we described so far is involved in action and intention understanding. From the very beginning of the studies of mirror neurons system, it was clear, however, that in humans motor system also “resonate” in response to intransitive movements, including those without any obvious meaning. Evidence for this came mostly from TMS studies (e.g., Refs. 17, 24, 61).

Fadiga et al. (17) asked volunteers to observe an experimenter grasping objects or performing meaningless arm gestures. As control, the detection of the dimming of a small spot of light was used. The results showed that observation of both transitive and intransitive actions produced an increase in the motor-evoked potentials (MEPs) recorded from the observer’s hand and arm muscles. The increase was found in those muscles that the participants would use to produce the movement observed. These findings were confirmed by other experiments in which proximal and distal movements were studied (see Ref. 50).

The existence of an intransitive movements mirror system is very relevant for understanding the neural basis of imitation. The term imitation has many definitions. There are, however, two main senses in which it is most commonly used. The first defines imitation as the capacity of an individual to replicate an observed motor act (49); the second defines imitation as the capacity to acquire, by observation, a new motor

behavior and to repeat it using the same movements employed by the teacher (62). In both cases, imitation requires the capacity to transform sensory information into a motor copy of it, including the capacity to imitate intransitive movements.

“The existence of an intransitive movements mirror system is very relevant for understanding the neural basis of imitation.”

Several experiments provide evidence that mirror mechanism is involved in imitation as an immediate replica of the observed motor act. Iacoboni et al. (29) tested volunteers in two main conditions: “observation” and “observation execution.” In the observation condition, participants were shown a moving finger, a cross on a stationary finger, or a cross on empty background. The instruction was to observe the stimuli. In the observation execution condition, the same stimuli were presented, but this time the instruction was to lift the right finger, as fast as possible, in response to them. The crucial contrast between the trials was in which the volunteers made the movement in response to an observed action (imitation) and in which the movement was triggered by the cross (a non-imitative behavior). The results showed that the activation of the mirror system and in particular of the posterior part of IFG was stronger during imitation.

Further evidence that the mirror system plays a fundamental role in this type of imitation was provided by repetitive TMS (rTMS), a technique that provokes a transient depression of the stimulated region. In a group of volunteers, Heiser et al. (27) stimulated the caudal part of the left frontal gyrus (Broca’s area) while they 1) pressed keys on a keyboard, 2) pressed the keys in response to a point of red light indicating which key to press, 3) imitated a key-pressing movement done by another individual. The data showed that rTMS lowered the participants’ performance during imitation but not during the other two tasks.

More complex appears to be mechanisms involved in imitation learning. In this case imitation appears to result from the interaction of two distinct processes: 1) segmentations of the action to be imitated into its individual elements and their transformation into the corresponding potential movements and motor acts of the observer; 2) organization of these potential movements and motor acts into a temporal and spatial pattern that replicates that shown by the demonstrator (7). There is evidence that the first step is carried out by the mirror system, whereas the second step is mostly due to the activity of the prefrontal lobe and in particular of *area 46* that memorizes and recombines the motor elements in the new pattern (5, 64).

Mirror Neurons and Speech

Although there is strong disagreement on whether human speech has its evolutionary roots in gestures or animals calls, nobody denies that speech is something more than a mere collection of curious sounds. This was clearly demonstrated by Liberman and colleagues (35, 36, 37) who showed that one cannot build an efficient communication system by simply using tone combinations. According to them, the unique property of speech is due to the capacity of speech sound to elicit the motor representation of the heard sound in the listener. There is evidence that this capacity has a precise neural correlate.

In a TMS experiment, Fadiga et al. (18) stimulated the left hemisphere speech motor centers and recorded MEPs from the tongue muscles in volunteers instructed to listen carefully to acoustically presented verbal and non-verbal material. The stimuli were words and bitonal sounds. In the middle of words, there was either a double “f” or a double “r.” “f” is a consonant that, when pronounced, requires virtually no tongue movements, whereas “r” is a consonant that, in contrast, requires marked tongue muscle involvement to be pronounced. The results showed that listening to words containing the double “r” produced a significant increase of MEPs amplitude recorded from tongue muscles compared with listening to bitonal sounds and words containing the double “f.”

Similar results were obtained by Watkins et al. (66). Using TMS technique, they recorded MEPs from a lip muscle and a hand muscle in four conditions: listening to continuous prose, viewing speech-related lip movements, listening to non-verbal sounds, and viewing eye and brow movements. Compared with viewing eye and brow movements, listening to and viewing speech enhanced the amplitude of MEPs recorded from the lip muscles. All of these effects were seen only in response to stimulation of the left hemisphere.

Taken together, these data indicate that, in humans, in addition to the mirror system transforming

observed intransitive movements into potential movements, there is a further system transforming heard phonemes in the corresponding motor representation of the same sound. There is no doubt that this system could play a fundamental role in language learning. It is matter of debate at what extent it intervenes in the comprehension of word meaning.

Mirror Neuron System and Emotion

There is no general agreement on what are the primal emotions. Some people narrow down emotions to five basic categories: love, happiness, anger, sadness, and fear. According to Darwin, another basic emotion is disgust (15), being that it is present in all human beings regardless of their race, gender, and social class.

Disgust is one of the emotions most investigated in neurophysiological studies. Brain imaging studies showed that when an individual is exposed to disgusting odors or tastes, there is an intense activation of two structures: the amygdala and the insula (2, 54, 56, 67).

The insula is a complex structure. It is formed by two major functional sectors: an anterior sector comprising the agranular and anterior disgranular insula and a posterior sector comprising the posterior disgranular and the granular insula. Its anterior sector receives a rich input from olfactory and gustatory centers and appears to control visceral and autonomic responses. Additionally, it receives visual information from the STS region (39). The posterior sector of the insula is characterized by connections with auditory, somatosensory, and premotor areas. From these data, it is clear that the insula is not exclusively a sensory area. Furthermore, in both monkeys and humans, its electrical stimulation may produce body movements typically accompanied by autonomic and visceromotor responses (34, 45, 57).

On the basis of brain-imaging studies (47, 56, 59, 60, 69) showing that, in humans, the observation of faces showing disgust activates the anterior insula, Wicker et al. (67) investigated in an fMRI study whether the insula sites that show activation during the experience of disgust also show activation during the observation of faces expressing disgust.

The study consisted of two sessions. In the first, the participants were exposed to unpleasant and pleasant odors; in the second, they watched a video showing the face expression of people sniffing an unpleasant, a pleasant, or a neutral odor. Three main structures became active during the exposure to smells: the amygdala, the insula, and the anterior cingulate. The amygdala was activated by both unpleasant and pleasant odors. In the insula, pleasant odors produced a relatively weak activation located in a posterior part of the right insula, whereas disgusting odors activated the anterior sector bilaterally. The results of visual runs showed activations in various cortical and

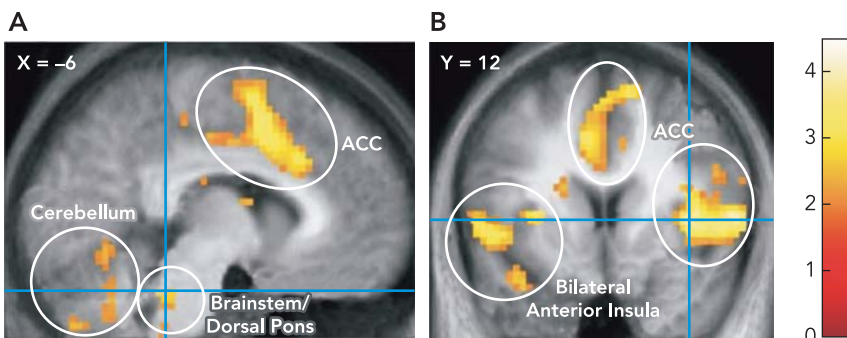


FIGURE 4. Activations found when pain was applied to self or to the partner

A and B: the results of a conjunction analysis between the contrasts of pain and no pain in the context of self and other. Results are shown on sagittal (A) and coronal (B) sections of the mean structural scan. Coordinates refer to peak activations. Increased pain-related activation was observed in the anterior cingulate (ACC), anterior insula, cerebellum, and brain stem (from Ref. 58).

subcortical centers but not in the amygdala. The left anterior insula and the anterior cingulate were activated only during the observation of disgust.

The most important result of the study was the demonstration that precisely the same foci within the anterior insula that were activated by the exposure to disgusting odorants were also activated by the observation of disgust. This finding strongly suggests that the insula and the anterior cingulate contain neural populations that becomes active both when the participants experience disgust and when they see it in others.

Because there are no data on single neuron properties of insula neurons during observation and feeling of disgust, it is possible to postulate that, instead of containing neurons endowed with a mirror mechanism, the insula and cingulate sites commonly activated by feeling and observing disgusting facial expressions contain two neuronal populations, one responding to the observation of emotional stimuli and the other active firing in association to the visceromotor expression of the same emotions. It is rather unlike, however, the mechanism for understanding how “hot” actions are radically different from “cold” actions, and the fact that the two putative populations of the insula and the anterior cingulate do not interact. Furthermore, at least for the cingulate cortex, there is evidence, although limited to one neuron, of a mirror mechanism identical to that described for the monkey parietal and premotor cortex (28).

In addition to disgust, activations in the anterior insula and in the anterior cingulate cortex were also obtained in studies in which emotional reactions to pain were investigated using an event-related fMRI paradigm (Ref. 58; see also Ref. 16). In this study, there were two conditions. In one, the participants were subjected to a mildly painful electric shock from electrodes placed on their hand; in the second, they were asked to watch while the same electrodes were positioned to the hand of a loved one. They were told that the loved person would receive the same shock to which they had been subjected earlier. The results showed that the same sites of the anterior insula and of the cingulate cortex became active in both conditions. This results show that both direct pain experience and its evocation are mediated by a mirroring similar to that found for disgust (FIGURE 4).

The hypothesis that emotions of others are recognized through an activation of those structures that mediate the feeling of that emotion in ourselves has been advanced by various authors (10, 11, 13, 23, 26). Particularly influential in this respect have been the studies by Damasio and his coworkers. According to these studies, mostly based on brain lesions, the neural basis of emotion understanding is the activation of an “as-if loop,” the core structure of which is the insula (1, 14). These authors attributed, at least in their initial studies, a role in the “as-if loop” also to somatosensory areas like SI and SII, conceiving the basis of experi-

ential emotion recognition to be in the activation in the observer of those cortical areas where the body is represented. Although a sensory contribution to emotion understanding is certainly possible, the activation of the rostral insula and, in contrast, the lack of the activation in the primary somatosensory cortices in emotion feeling strongly suggest a non-sensorial basis for emotion recognition.

Finally, it should be stressed that, although the notion that the activation of visceromotor structures provides the basis for the recognition of emotion, it does not exclude that emotions may be also recognized indirectly using cognition. Some particular visual features representing the basic features of an emotion, like in schematic faces, allows emotion recognition. This emotion recognition is, however, radically different from that mediated by the insula and the anterior cingulate, with only the latter creating a shared feeling between the observer and the person actually feeling the emotion.

Conclusions

The direct transformation of sensory information into a motor format (mirror mechanism) plays an important role in many cognitive functions ranging from understanding motor acts to understanding intentions, and from experiencing others’ emotions to imitation and speech. This variety of functions in which mirroring is involved sometimes elicits surprise, probably because many have in mind only the properties of mirror neurons of area F5. These neurons, however, are only a type of neurons endowed with mirror properties. In these last few years, a large body of evidence accumulated that shows that mirror mechanism is also present in other cortical areas and that, according to the anatomical network where it is located, mirror mechanism may mediate a variety of cognitive functions. Thus, besides the parieto-frontal mirror system involved in action and intention understanding, there are other mirror systems involved in copying intransitive movements, in transforming phonemes into the motor pattern for phonemes production, and in emotion recognition. It likely that this list of mirror systems is by no means exhaustive and that future research will discover other networks endowed with the mirror mechanism. ■

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