

# Mirror neuron: a neurological approach to empathy

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## Summary

Humans are an exquisitely social species. Our survival and success depend critically on our ability to thrive in complex social situations. But how do we understand others? Which are the mechanisms underlying this capacity?

In the present essay we discuss a general neural mechanism (“mirror mechanism”) that enables individuals to understand the meaning of actions done by others, their intentions, and their emotions, through activation of internal representations coding motorically the observed actions and emotions.

In the first part of the essay we will show that the mirror mechanism for “cold” actions, those devoid of emotional content, is localized in parieto-frontal cortical circuits. These circuits become active both when we do an action and when we observe another individual doing the same action. Their activity allows the observer to understand the “what” of an action.

We will show, then, that a “chained” organization of motor acts plus the mirror mechanism enable the observer to understand the intention behind an action (the “why” of an action) by observing the first motor act of an action.

Finally, we will discuss some recent data showing that the mirror mechanism localized in other centers, like the insula, enables the observer to understand the emotions of others. We will conclude briefly discussing whether these biological data allow inferences about moral behavior.

## Introduction

“How selfish soever man may be supposed, there are evidently some principles in his nature, which interest him in the fortune of others, and render their happiness necessary to him, though he derives nothing from it except the pleasure of seeing it.” This famous sentence by Adam Smith (1759), which so nicely describes our empathic relation with others, contains two distinct concepts.

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The first is that individuals are endowed with a mechanism that makes them share the “fortunes” of others. By observing others, we enter in an “empathic” relation with them. This empathic relation concerns not only the emotions that others feel but also their actions. “The mob, when they are gazing at a dancer on the slack rope, naturally writhe and twist and balance their own bodies, as they see him do, and as they feel that they themselves must do if in his situation.” (Smith 1759).

The second idea is that, because of our empathy with others, we are compelled to desire their happiness. If others are unhappy, we are also unhappy, because the other’s unhappiness somehow intrudes into us.

According to Smith, the way in which we enter into empathic relation may be voluntary (“As we have no immediate experience of what other men feel, we can form no idea of the manner in which they are affected, but by conceiving what we ourselves should feel in the like situation”), but also, as shown in the above-cited example of the “dancer,” may be automatically triggered by the observation of the behavior of others.

The aim of this essay is to discuss the existence of a neural mechanism, resembling that described by Adam Smith, that puts the individual in empathic contact with others. This mechanism – the mirror mechanism – enables the observer to understand the actions of others, the intention behind their actions, and their feelings. In a short “coda,” we will discuss the validity of the second idea of Adam Smith, the obligatory link between our happiness and that of others.

## Action understanding

Humans are social beings. They spend a large part of their time observing others and trying to understand what they are doing and why. Not only humans but also apes and monkeys have a strongly developed interest in others.

How are actions recognized? The traditional view is that action recognition is based exclusively on the visual system. The understanding of an action done by another individual depends on the activity of the higher order visual areas and, in particular, of those of the superior temporal sulcus, where there are neurons selectively activated by biological motions (Perrett et al. 1989; Carey et al. 1997; Allison et al. 2000; Puce and Perrett 2003).

Another hypothesis is that an action is recognized when the observed action activates, in the observer’s brain, an analogous motor representation. The observer does not execute that action, because control mechanisms prevent its overt occurrence, but the evoked motor representation (“motor knowledge”) allows him to understand the meaning of what he saw (Rizzolatti et al. 2001).

It is important to note that the two hypotheses are not in contraposition. Rather, they describe two different ways in which an action may be understood. The “visual” hypothesis describes a “third person” relation between the observer and the observed action. The action, albeit recognized in its general meaning, is not understood in all its implications, because it does not enter into the semantic motor network of the observing individual as well as in his/her private knowledge of what doing that action means. “Visual” understanding is similar to that a robot,

able to differentiate an action from another, may have, or humans have when they see a bird flying or a dog barking (see below). In contrast, the “motor” hypothesis describes the “first person” understanding of what the individual is seeing. The observed action enters into the observer’s motor representation and recalls his/her similar experiences when doing that action. It is an empathic recognition that makes the observer share the experience of the action agent.

## Mirror Neuron System and Action Understanding

The strongest evidence in favor of the “motor hypothesis” is represented by mirror neurons. These neurons, originally found in the monkey ventral premotor cortex (area F5), are active both when the monkey *does* a particular action and when it *observes* another individual doing a similar action. The mirror neurons do not respond to object presentation. Similarly, they do not respond to the sight of an agent mimicking actions or performing non-object-directed gestures. Mirror neurons have also been described in the monkey parietal lobe (Fogassi et al. 1998; Gallese et al. 2002).

The mirror mechanism appears to be a mechanism particularly well suited for imitation. Imitation, however, appeared only late in evolution. Monkeys, which have a well-developed mirror system, lack this capacity and even apes have it only in a rather rudimentary form (see Tomasello and Call 1997; Visalberghi and Frigaszy 2002).

The properties of monkey mirror neurons also indicate that this system initially evolved not for imitation. Mirror neurons typically show a good congruence between the visual actions they respond to and the motor responses they code, yet only in a minority of them do the effective observed and effective executed actions correspond in terms of *both* goal and means for reaching the goal. Most of them code the goal of the action (e.g., grasping) but not the way in which the observed action is done. These neurons are, therefore, of little use for imitation in the proper sense, that is the capacity to imitate an action as it has been performed (Rizzolatti and Craighero 2004).

Summing up, it is very likely that the faculty for imitation developed on the top of the mirror system. However, its initial basic function was not imitation but enabling an individual to understand actions done by others (see Rizzolatti et al. 2001).

Evidence in favor of the notion that mirror neurons are involved in action understanding comes from a recent series of studies in which mirror neurons were tested in experimental conditions in which the monkey could understand the meaning of an occurring action but had no visual information about it. The rationale of these studies was the following: if mirror neurons mediate action understanding, they should become active when the meaning of the observed action is understood, even in the absence of visual information.

The results showed that this is the case. In one study, F5 mirror neurons were recorded while the monkey was observing a “noisy” action (e.g., ripping a piece of paper) and then was presented with the same noise without seeing the action. The results showed that a large number of mirror neurons, responsive to the ob-

ervation of noisy actions, also responded to the presentation of the sound proper of that action, alone. Responses to white noise or to the sound of other actions were absent or much weaker than responses to the preferred action. Neurons responding selectively to specific action sounds were named “audio-visual” mirror neurons (Kohler et al. 2002).

In another study, mirror neurons were tested by introducing a screen between the monkey and the location of an object (Umiltà et al. 2001). The idea underlying the experiment was that, if mirror neurons are involved in action understanding, they should also discharge in conditions in which the monkey does not see the occurring action but has sufficient clues to create a mental representation of what the experimenter does. The monkeys were tested in four conditions: 1) the experimenter is grasping an object; 2) the experimenter is miming grasping, and 3) and 4), the monkey observes the actions of 1) and 2) but the final critical part of them (hand-object interaction) is hidden by a screen. It is known that mirror neurons typically do not fire during the observation of mimed actions. At the beginning of each “hidden” trial, the monkey was shown whether there was or was not an object behind the screen. Thus, in the hidden condition, the monkey “knew” that the object was present behind the screen and could mentally represent the action.

The results showed that more than half of the tested neurons discharged in the hidden condition, thus indicating that the monkey was able to understand the goal of the action even in the absence of the visual aspect describing the action.

In conclusion, both the experiments show that the activity of mirror neurons correlates with action understanding. The visual features of the observed actions are necessary to trigger mirror neurons only inasmuch as they allow the understanding of the observed actions. If action comprehension is possible on other bases, mirror neurons signal the action even in the absence of visual stimuli.

## **The Mirror Neuron System in Humans**

Evidence, based on single neuron recordings, of the existence of mirror neurons in humans is lacking. Their existence is, however, indicated by EEG and MEG studies, TMS experiments, and brain imaging studies (see Rizzolatti and Craighero 2004). For the sake of space, we will review here only a tiny fraction of these studies.

MEG and EEG studies showed that the desynchronization of the motor cortex observed during active movements was also present during the observation of action done by others (Hari et al. 1998; Cochin et al. 1999). Recently, desynchronization of cortical rhythms was found in functionally delimited language and hand motor areas in a patient with implanted subdural electrodes, both during observation and execution of finger movements (Tremblay et al. 2004).

TMS studies showed that the observation of actions done by others determines an increase of corticospinal excitability with respect to the control conditions. This increase concerned specifically those muscles that the individuals use for producing the observed movements (e.g., Fadiga et al. 1995; Strafella and Paus 2000; Gangitano et al. 2001, 2004).

Brain imaging studies allowed the localization of the cortical areas forming the human mirror neuron system. They showed that the observation of actions done by others activates, besides visual areas, two cortical regions whose function is classically considered to be fundamentally or predominantly a motor one: the inferior parietal lobule (area PF/PFG), and the lower part of the precentral gyrus (ventral premotor cortex) plus the posterior part of the inferior frontal gyrus (IFG). (Rizzolatti et al. 1996; Grafton et al. 1996; Grèzes et al. 1998, 2003; Iacoboni et al. 1999, 2001; Nishitani and Hari 2000, 2002; Buccino et al. 2001; Koski et al. 2002, 2003; Manthey et al. 2003, Johnson-Frey et al. 2003). These two regions form the core of the mirror neuron system in humans.

Recently, an fMRI experiment was carried out to see which type of observed actions is recognized using the mirror neuron system (Buccino et al. 2004). Video-clips showing silent mouth actions done by humans, monkeys and dogs were presented to normal volunteers. Two types of actions were shown: biting and oral communicative actions (speech reading, lip-smacking, barking). Static images of the same actions were presented as a control.

The results showed that the observation of biting, regardless of whether done by a man, a monkey or a dog, determined the same two activation foci in the inferior parietal lobule, and in the *pars opercularis* of IFG and the adjacent precentral gyrus. Speech reading activated the left *pars opercularis* of IFG, whereas the observation of lip smacking activated a small focus in the right and left *pars opercularis* of IFG. Most interestingly, the observation of barking *did not* produce any mirror neuron system activation.

These results strongly support the notion mentioned above that actions done by other individuals can be recognized through different mechanisms. Actions belonging to the motor repertoire of the observer are mapped on his/her motor system. Actions that do not belong to this repertoire do not excite the motor system of the observer and appear to be recognized essentially on a visual basis. Thus, in the first case, the motor activation translates the visual experience into an empathic, first person knowledge, whereas this knowledge is lacking in the second case.

## Intention understanding

The data discussed above indicate that the premotor and parietal cortices of primates contain a mechanism that allows individuals to understand the actions of others. Typically, an individual observing an action done by another person not only understands what that person is doing, but also why he/she is doing it. Let us imagine a boy grasping a mug. There are many reasons why the boy could grasp it, but the observer usually is able to infer why he did it. For example, if the boy grasped the cup by the handle, it is likely that he wants to drink the coffee, while if he grasped it by the top it is more likely that he wants to place it in a new location.

The issue of whether the intention comprehension (the “why” of an observed action) could be mediated by the mirror neurons has been recently addressed in a study in which the motor and visual properties of mirror neurons of the infe-

rior parietal lobule (IPL) were investigated (Fogassi et al., manuscript in preparation).

IPL neurons that discharge during active grasping were selected. Subsequently, their motor activity was studied in two main conditions. In the first, the monkey grasped a piece of food located in front of it and brought it to its mouth (eating condition). In the second, the monkey grasped an object and placed it into a container (placing condition).

The results showed that the large majority of IPL grasping neurons (about 65% of them) were significantly influenced by the action in which the grasping was embedded. Examples are shown in Figure 1. Neurons coding grasping for eating were much more common than neurons coding grasping for placing, with a ratio of two to one.

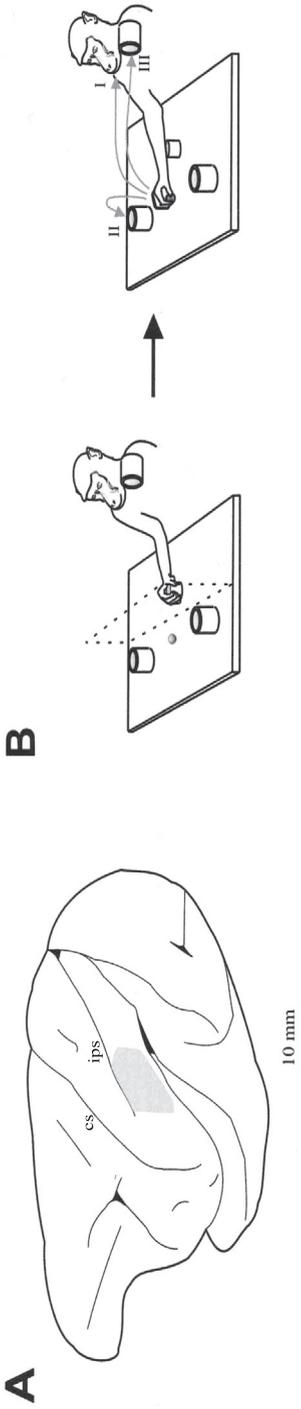
Studies in humans showed that the kinematics of the first motor act of an action is influenced by the subsequent motor acts of that action (see Jeannerod 1988). The recordings of reaching-to-grasp kinematics of the monkeys in the two experimental conditions described above confirmed these findings. Reaching-to-grasp movement followed by arm flexion (bringing the food to the mouth) was faster than the same movement followed by arm abduction (placing the food into the container). To control for whether the differential discharge of grasping neurons in eating and placing conditions were due to this difference in kinematics rather than to the action goal, a new placing condition was introduced (see Fig. 1). In this condition the monkey had to grasp a piece of food and place it into a container located near its mouth. Thus, the new place condition was identical in terms of goal to the original one but required, after grasping, arm flexion rather than arm abduction. The kinematics analysis of the reaching-to-grasp movement showed that the wrist peak velocity was fastest in the new placing condition, intermediate in the eating condition, and slowest in the original placing condition.

Neuron activity showed that, regardless of arm kinematics, the neuron selectivity remained unmodified. Neurons selective for placing in the far container showed the same selectivity for placing in the container near the monkey's mouth. Thus, it is the goal of the action that determines the motor selectivity of IPL neurons in coding a given motor act, rather than factors related to movement kinematics.

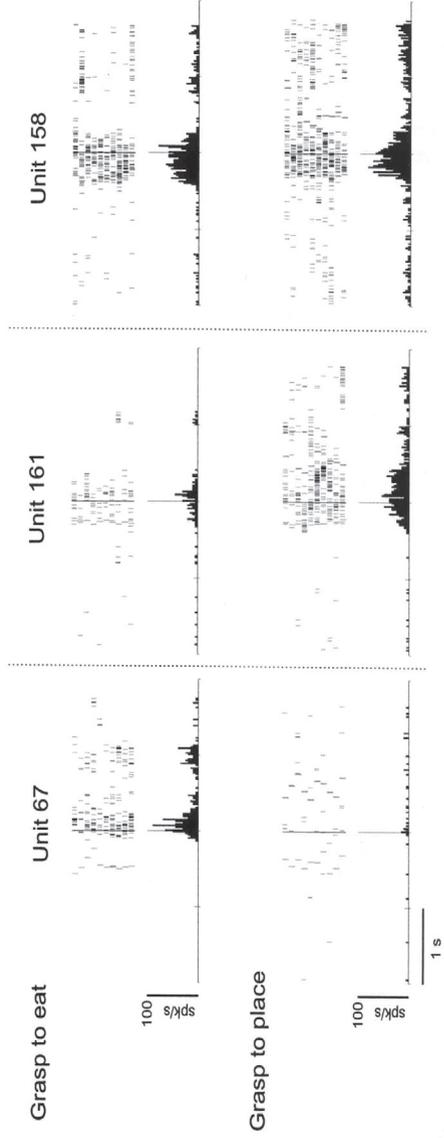
As in the premotor cortex, there are neurons in IPL that are endowed with mirror properties, discharging both during the observation and execution of the

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**Fig. 1. A.** Lateral view of the monkey brain showing the sector of IPL (gray shading) from which the neurons were recorded; cs, central sulcus; ips, inferior parietal sulcus. **B** Schematic drawing illustrating the apparatus and the paradigm used for the motor task. Left: starting position of the task. A screen prevents the monkey from seeing the target. Right: after the screen is removed, the monkey could release the hand from the starting position, reach and grasp the object to bring it to its mouth (Condition I) or to place it into a container located near the target (II) or near its mouth (III). **C** Activity of three IPL neurons during grasping in Conditions I and II. Rasters and the histograms are synchronized with the moment when the monkey touched the object to be grasped. Red bars indicate the moment when the monkey released its hand from the starting position. Green bars indicate the moment when the monkey touched the container. Abscissa: time, bin = 20 ms; ordinate: discharge frequency. (From Fogassi et al., in preparation)



**C** Motor responses of parietal neurons



same motor act (Fogassi et al. 1998, Gallese et al. 2002). To see whether these neurons also discharge differentially during the observation of the same motor act but embedded in different actions, their visual properties were tested in the same two conditions as those used for studying their motor properties. The actions were performed by an experimenter in front of the monkey. In one condition, the monkey observed the experimenter grasping a piece of food and bringing it to his mouth; in the other, the monkey observed the experimenter placing an object into the container.

The results showed that more than two-thirds of IPL neurons were differentially activated during the observation of grasping in placing and eating conditions. Examples are shown in Figure 2. Neurons responding to the observation of grasping for eating were more represented than neurons responding to the observation of grasping for placing, again with a two to one ratio.

A comparison between neuron selectivity during the execution of a motor act and motor act observation showed that the great majority of neurons (84%) have the same specificity during grasping execution and grasping observation. Thus, a mirror neuron whose discharge was higher during the observation of grasping for eating than during the observation of grasping for placing also had a higher discharge when the monkey grasped for eating than when it grasped for placing. The same was true for neurons selective for grasping for placing.

The motor and visual organization of IPL, just described, is of great interest for two reasons. First, it indicates that motor actions are organized in the parietal cortex in specific chains of motor acts; second, it strongly suggests that this chained organization might constitute the neural basis for understanding the intentions of others.

In favor of the existence of action chains in IPL, it is not only the activation of neurons coding the same motor act in one condition and not in another, but also the organization of IPL neuron-receptive fields. This organization shows that there is a predictive facilitatory link between subsequent motor acts. To give an example, there are IPL neurons that respond to the passive flexion of the forearm, have tactile receptive fields on the mouth, and in addition discharge during mouth grasping (Ferrari et al., manuscript in preparation). These neurons facilitated the mouth opening when an object touched the mouth, but also when the monkey grasped it, producing a contact between the object and the hand tactile-receptive field. Recently, several examples of predictive chained organization in IPL have been described by Yokochi et al. (2003). If one considers that a fundamental aspect of action execution is its fluidity, the link between the subsequent motor acts forming an action and the specificity of neurons coding them appears to be an optimal solution for executing an action without intervening pauses between the individual motor acts forming it.

The presence of chained motor organization of IPL neurons has deep implications for intention understanding. The interpretation of the functional role of mirror neurons, as described above, was that of action understanding. A motor act done by another individual is recognized when this act triggers the same set of neurons that are active during that act execution. The action-related IPL mirror neurons allow one to extend this concept. These neurons discriminate one motor act from another, thus activating a motor act chain that codes the final goal of the

action. In this way the observing individual may re-enact internally the observed action and thus *predict* the goal of the observed action. In this way, the observer can “read” the intention of the acting individual.

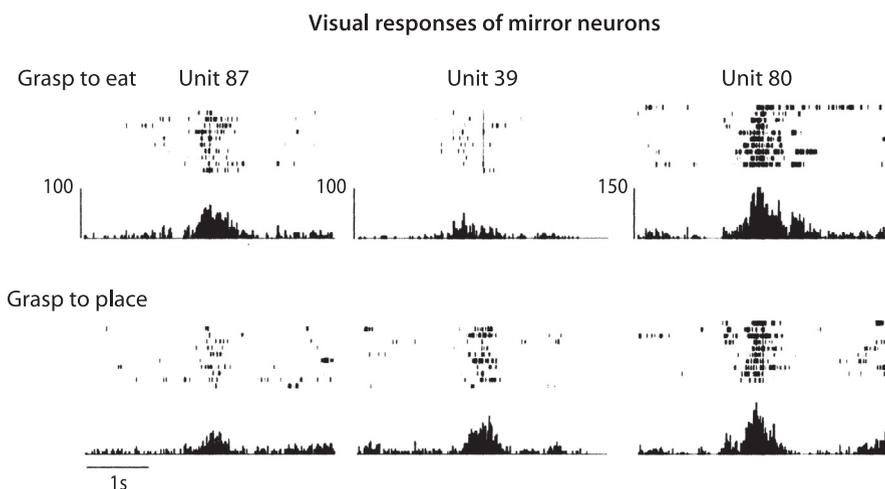
This intention-reading interpretation predicts that, in addition to mirror neurons that fire during the execution and observation of the same motor act (“classical mirror neurons”), there should be neurons that are visually triggered by a given motor act but discharge during the execution *not* of the same motor act, but of another one that is functionally related to the former and part of the same action chain. Neurons of this type have been previously described both in F5 (Di Pellegrino et al. 1992) and in IPL (Gallese et al. 2002) and referred to as “logically related” mirror neurons. These “logic” mirror neurons were never theoretically discussed because their functional role was not clear. The findings just discussed allow us to not only account for their occurrence but also to indicate their necessity, if the chain organization is at the basis of intention understanding.

While the mechanism of intention understanding just described appears to be rather simple, it would be more complex to specify how the selection of a particular chain occurs. After all, what the observer sees is just a hand grasping a piece of food or an object.

There are various factors that may determine this selection. The first is the context in which the action is executed. In the study described above, the clue for possible understanding of the intention of the acting experimenter was either the presence of the container (placing condition) or its absence (eating condition). The second factor that may intervene in chain selection is the type of object that the experimenter grasped. Typically, food is grasped in order to be eaten. Thus, the observation of a motor act directed towards food is more likely to trigger grasping-for-eating neurons than neurons that code grasping for other purposes. This food-eating association is, of course, not mandatory but could be modified by other factors.

One of these factors is the standard repetition of an action. Another is, as mentioned before, the context in which the action is performed. Context and object type were found to interact in some neurons. For example, some neurons that selectively discharged during the observation of grasping for eating also discharged, although weakly, during the observation of grasping for placing when the object to be placed was food, but not when it was a solid. It was as if the eating chain was activated, although slightly, by food in spite of the presence of a contextual clue indicating that placing was the most likely action. A few neurons, instead of showing an intermediate discharge when the nature of the stimulus (food) and context conflicted, decreased their discharge with time when the same action was repeated. It was as if the activity of the placing chain progressively inhibited the activity of neurons of the eating chain.

Understanding “other minds” constitutes a special domain of cognition. Developmental studies clearly show that this cognitive faculty has various components and that there are various steps through which infants acquire it (see Saxe et al. 2004). Brain imaging studies also tend to indicate the possibility of an involvement of many areas in this function (Blakemore and Decety 2001; Frith and Frith 2003; Gallagher and Frith 2003).



**Fig. 2.** Visual responses of IPL mirror neurons during the observation of grasping-to-eat and grasping-to-place done by an experimenter. Conditions as in Figure 1. (From Fogasso et al., in preparation)

Given the complexity of the problem, it would be naive to claim that the mechanism described in the present study is *the* mechanism at the basis of mind reading. Yet, the present data show for the first time a neural mechanism through which an important aspect of mind reading, understanding the intention of others, may be solved.

## Emotion understanding

Up to now we have dealt with the neural mechanisms that enable individuals to understand “cold actions,” that is, actions without any obvious emotional content. In social life, however, equally important, and maybe even more so, is the capacity to decipher emotions. Which mechanisms enable us to understand what others feel? Is there a mirror mechanism for emotions similar to that for cold action understanding?

It is reasonable to postulate that, as for action understanding, there are two basic mechanisms for emotion understanding that are conceptually different one from another. The first consists in cognitive elaboration of sensory aspects of others’ emotional behaviors. The other consists in a direct mapping of sensory aspects of the observed emotional behavior on the motor structures that determine, in the observer, the experience of the observed emotion.

These two ways of recognizing emotions are experientially radically different. With the first, the observer understands the emotions expressed by others but does not feel them. He deduces them. A certain facial or body pattern means

fear, another happiness, and that is it. No emotional involvement. Different is the case for sensory-motor mapping mechanism. In this case, the recognition occurs because the observed emotion triggers the feeling of the same emotion in the observing person. It is a first-person recognition. The emotion of the other penetrates the emotional life of the observer, evoking in him/her not only the observed emotion but also related emotional states and nuances of similar experiences.

As for cold action, our interest in this essay is the mechanisms underlying the direct sensory-motor mapping. For the sake of space, we will review data on one emotion only – disgust – for which rich empirical evidence has been recently acquired.

Disgust is a very basic emotion whose expression has an important survival value for the conspecifics. In its most basic, primitive form (“core disgust;” Rozin et al. 2000) disgust indicates that something (e.g., food) that the individual tastes or smells is bad and, most likely, dangerous. Because of its strong communicative value, disgust is an ideal emotion for testing the direct mapping hypothesis.

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 (Augustine 1996; Royet et al. 2003; Small et al. 2003; Zald et al. 1998; Zald and Pardo 2000). The amygdala is a heterogeneous structure formed by several subnuclei. Functionally, these subnuclei form two major groups: the corticomедial group and the basolateral group. The former, phylogenetically more ancient, is related to the olfactory modality. It is likely that it is the signal increase in the corticomедial group that is responsible for the amygdala activation in response to disgusting stimuli.

Similarly to the amygdala, the insula is a heterogeneous structure. Anatomical connections revealed two main functional subdivisions: an anterior “visceral” sector and a multimodal posterior sector (Mesulam and Mufson 1982). The anterior sector receives a rich input from olfactory and gustatory centers. In addition, the anterior insula receives an important input from the inferotemporal lobe, where, in the monkey, neurons have been found to respond to the sight of faces (Gross et al. 1972; Tanaka 1996). Recent data demonstrated that the insula is the main cortical target of interoceptive afferents (Craig 2002). Thus, the insula is not only the primary cortical area for chemical exteroception (e.g., taste and olfaction) but also for the interoceptive state of the body (“body state representation”).

The insula is not an exclusively sensory area. In both monkeys and humans, electrical stimulation of insula produces body movements (Kaada et al. 1949; Penfield and Faulk 1955; Frontera 1956; Showers and Lauer 1961; Krolak-Salmon et al. 2003). These movements, unlike those evoked by stimulation of classical motor areas, are typically accompanied by autonomic and visceromotor responses.

Functional imaging studies in humans showed that, as in the monkey, the anterior insula receives, in addition to olfactory and gustatory stimuli, higher order visual information. Observation of disgusted facial expressions produces signal increase in the anterior insula. (Phillips et al. 1997, 1998; Sprengelmeyer et al. 1998; Schienle et al. 2002).

Recently, Wicker et al. (2003) carried out an fMRI study in which they tested whether the *same* insula sites that show signal increase during the experience of

disgust also show signal increase during the observation of facial expressions of disgust.

The study consisted of olfactory and visual runs. In the olfactory runs, individuals inhaled disgusting and pleasant odorants. In the visual runs, the same participants viewed video-clips of individuals smelling a glass containing disgusting, pleasant and neutral odorants and expressing their emotions.

Disgusting odorants produced, as expected, a very strong signal increase in the amygdala and in the insula, with a right prevalence. In the amygdala, activation was also observed with pleasant odorants, with a clear overlap between the activations obtained with disgusting and pleasant odorants. In the insula, pleasant odorants produced a relatively weak activation located in a posterior part of the right insula; disgusting odorants activated the anterior sector bilaterally. The results of visual runs showed signal increases in various cortical and subcortical centers but not in the amygdala. The insula (anterior part, left side) was activated only during the observation of disgust.

The most important result of the study was the demonstration that precisely the same sector within the anterior insula that was activated by the exposure to disgusting odorants was also activated by the observation of disgust in others (Fig. 3). These data strongly suggest that the insula contains neural populations that become active both when the participants experience disgust and when they see it in others.

The notion that the insula mediates both recognition and experience of disgust is supported by clinical studies showing that, following lesions of the insula, patients have a severe deficit in understanding disgust expressed by others (Calder

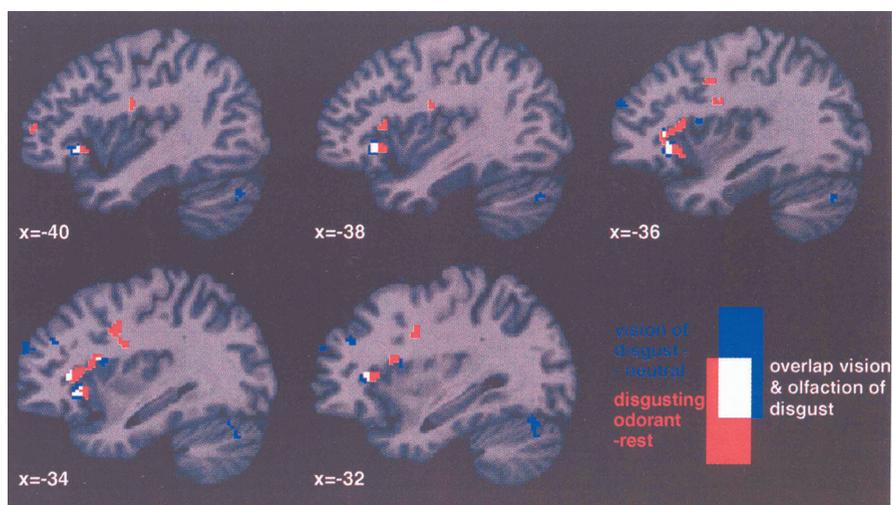


Fig. 3. Illustration of the overlap (white) between the brain activation during the observation (blue) and the feeling (red) of disgust. The olfactory and visual analyses were performed separately as random-effect analyses. The results are superimposed on parasagittal slices of a standard MNI brain.

et al. 2000; Adolphs et al. 2003). This deficit is accompanied by blunted and reduced sensation of disgust. In addition, electrophysiological studies showed that sites in the anterior insula, whose electrical stimulation produced unpleasant sensations in the patient's mouth and throat, are activated by the observation of a face expressing disgust.

Taken together, these data strongly suggest that humans understand disgust, and most likely other emotions (see Carr et al. 2003, Singer et al., 2004), through a direct mapping mechanism. The observation of emotionally laden actions activates those structures that give a first-person experience of the same actions. By means of this activation, a bridge is created between others and us.

The hypothesis that we perceive emotion in others by activating the same emotion in ourselves has been advanced by various authors (e.g., Phillips et al. 1997; Adolphs 2003; Damasio 2003a; Calder et al, 2000; Carr et al. 2003; Goldman and Sripada 2003; Gallese et al. 2004). Particularly influential in this respect has been the work by Damasio and his coworkers (Adolphs et al. 2000; Damasio 2003a, b) According to these authors, the neural basis of empathy is the activation of an "as-if-loop," the core structure of which is the insula (Damasio 2003). These authors attributed a role in the "as-if-loop" also to somatosensory areas like SI and SII, conceiving the basis of empathy to be in the activation in the observer of those cortical areas where the body is represented.

Although this hypothesis is certainly possible, the crucial role of the insula, rather than of the primary somatosensory cortices, in emotion feeling strongly suggests that the neural substrate for emotions is not merely sensorial. It is more likely that the activation of the insula representation of the visceromotor activity is responsible for the first-person feeling of disgust. As for the premotor cortex, it is plausible that in the insula there is a specific type of mirror neurons that match the visual aspect of disgust with its visceromotor aspects. The activation of these (hypothetical) visceromotor mirror neurons should underlie the first-person knowledge of what it means to be disgusted. The activation of these insular neurons should not necessarily produce the overt visceromotor response. The overt response should depend on the strength of the stimuli and other factors. A neurophysiological study of insula neuron properties could be the direct test of this hypothesis.

## Coda

The data reviewed in this essay show that the intuition of Adam Smith – that individuals are endowed with an altruistic mechanism that makes them share the "fortunes" of others – is strongly supported by neurophysiological data. When we observe others, we enact their actions inside ourselves and we share their emotions.

Can we deduce from this that the mirror mechanism is the mechanism from which altruistic behavior evolved? This is obviously a very hard question to answer. Yet, it is very plausible that the mirror mechanism played a fundamental role in the evolution of altruism. The mirror mechanism transforms what others do and feel in the observer's own experience. The disappearance of unhappi-

ness in others means the disappearance of unhappiness in us and, conversely, the observation of happiness in others provides a similar feeling in ourselves. Thus, acting to render others happy – an altruistic behavior – is transformed into an egoistic behavior – we are happy.

Adam Smith postulated that the presence of this sharing mechanism renders the happiness of others “necessary” for human beings, “though he derives nothing from it except the pleasure of seeing it.” This, however, appears to be a very optimistic view. In fact, an empathic relationship between others and ourselves does not necessarily bring positive consequences to the others. The presence of an unhappy person may compel another individual to eliminate the unpleasant feeling determined by that presence, acting in a way that is not necessarily the most pleasant for the unhappy person.

To use the mirror mechanism – a biological mechanism – strictly in a positive way, a further – cultural – addition is necessary. It can be summarized in the prescription: “Therefore all things whatsoever ye would that men should do to you, do ye even so to them: for this is the law and the prophets” (Matthew 7, 12). This “golden rule,” which is present in many cultures besides ours (see Changeux and Ricoeur 1998), uses the positive aspects of a basic biological mechanism inherent in all individuals to give ethical norms that eliminate the negative aspects that are also present in the same biological mechanism.

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