

A unifying view of the basis of social cognition

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In this article we provide a unifying neural hypothesis on how individuals understand the actions and emotions of others. Our main claim is that the fundamental mechanism at the basis of the experiential understanding of others' actions is the activation of the mirror neuron system. A similar mechanism, but involving the activation of visceromotor centers, underlies the experiential understanding of the emotions of others.

Humans are an exquisitely social species. Our survival and success depends crucially on our ability to thrive in complex social situations. One of the most striking features of our experience of others is its intuitive nature. This implicit grasp of what other people do or feel will be the focus of our review. We will posit that, in our brain, there are neural mechanisms (mirror mechanisms) that allow us to directly understand the meaning of the actions and emotions of others by internally replicating ('simulating') them without any explicit reflective mediation. Conceptual reasoning is not necessary for this understanding. As human beings, of course, we are able to reason about others and to use this capacity to understand other people's minds at the conceptual, declarative level. Here we will argue, however, that the fundamental mechanism that allows us a direct experiential grasp of the mind of others is not conceptual reasoning but direct simulation of the observed events through the mirror mechanism. The novelty of our approach consists in providing for the first time a neurophysiological account of the experiential dimension of both action and emotion understanding.

What makes social interactions so different from our perception of the inanimate world is that we witness the actions and emotions of others, but we also carry out similar actions and we experience similar emotions. There is something shared between our first- and third-person experience of these phenomena: the observer and the observed are both individuals endowed with a similar brain-body system. A crucial element of social cognition is the brain's capacity to directly link the first- and third-person experiences of these phenomena (i.e. link 'I do and I feel' with 'he does and he feels'). We will define this mechanism 'simulation'.

In the first part of this review we will show that in the case of actions, simulation is based on a neural system

responding both when we execute a particular goal-directed action and when we observe someone else performing a similar action (mirror neuron system). In the second part, we will show that a similar mirroring mechanism, bridging first- and third-person experiences, also exists for emotions.

Action understanding: cognitive and motor mechanisms

The conventional conceptual approach for understanding actions performed by others is to consider seen actions in a similar way to all other visual stimuli. Let us imagine a boy throwing stones into a river: the visual system describes the boy, the stone, the river, the movement of his arm, and the flying of the stones. The integration of all these separate elements produces the neural input to a central conceptual system that will interpret and assign meaning to the visual representation (e.g. see Fodor [1,2]).

In recent years, a different proposal has been advanced on how others' actions can be understood. This proposal is mostly based on the discovery of a set of neurons called 'mirror neurons'. These neurons, originally found in the ventral premotor cortex (area F5) of the macaque monkey, respond both when the monkey performs a particular goal-directed action, and when it observes another individual performing a similar action [3,4]. The core of the proposal is that the observation of an action leads to the activation of parts of the same cortical neural network that is active during its execution. The observer understands the action because he knows its outcomes when he does it. Action understanding does not depend, according to this view, on the activation of visual representations (an activation obviously present) followed by their interpretation by the central conceptual system, but by the 'penetration' of visual information into the experiential ('first person') motor knowledge of the observer.

Evidence for motor involvement in action understanding: monkey data

In addition to previous evidence (see above), the proposed link between action understanding and observer's motor activation was recently supported by two studies on mirror neuron properties. In both of them, the activity of F5 mirror neurons was studied in conditions in which the monkey could understand the meaning of the occurring action, but had no access to the visual features that typically trigger mirror neurons. If mirror neurons mediate action understanding, one should also expect

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their activation in these conditions, reflecting the meaning of the observed action.

In the first study, mirror neurons were tested in two conditions: in one, the monkey could see the entire action (e.g. a hand grasping action); in the other, the same action was presented but its final critical part, that is the hand-object interaction, was hidden by a screen (Figure 1). Thus, in the hidden condition the monkey only 'knew' that the object was present behind the screen. The results showed that more than half of the recorded neurons also responded in the hidden condition [5].

In the second study, F5 mirror neurons were recorded when the monkey saw and heard executed noisy actions (e.g. breaking peanuts, tearing sheets of paper apart), only saw, or only heard the same actions performed by another individual (Figure 2). Like all F5 mirror neurons, the mirror neurons in this study had motor properties and fired during execution of those actions, the observation of which also triggered their activation. The results showed that about 15% of mirror neurons responsive to presentation of actions accompanied by sounds also responded to the presentation of the sound alone. These 'audiovisual mirror neurons' therefore represent actions independently of whether these actions are performed, heard or seen [6].

These studies suggest that the activity of mirror neurons correlates with action understanding. The sensory features of the perceived actions (partially seen or just heard) are fundamental to the activation of mirror neurons only inasmuch as they trigger the motor representation of the same actions within the observer/listener brain.

Evidence for motor involvement in action understanding: human data

Several studies using different methodologies have shown that, in humans too, the observation of actions performed by others activates cortical motor representations. The human mirror neuron system is formed by a cortical network composed of the rostral part of the inferior parietal lobule and by the caudal sector (*pars opercularis*) of the inferior frontal gyrus (IFG), plus the adjacent part of the premotor cortex (see [7]).

The human mirror neuron system 'resonates' in response to a wider range of actions than the monkey system. First, whereas the presence of an object – the target of the action – appears to be necessary to activate the mirror neuron system in the monkey [3,4], the observation of intransitive and mimed actions is able to activate the human system [8–10]. Second, TMS experiments have shown that, in humans, motor evoked potentials (MEPs) recorded from the muscles of an observer, are facilitated when an individual observes intransitive, meaningless hand/arm gestures, as well as when an individual observes a transitive action [11,12]. Taken together, these data show that the human motor system codes both the goal of an observed action and the way in which the observed action is performed.

In summary, these data indicate that when we see someone performing an action, besides the activation of various visual areas, there is a concurrent activation of part of the same motor circuits that are recruited when we ourselves perform that action. Although we do not overtly

reproduce the observed action, part of our motor system becomes active 'as if' we were executing that very same action that we are observing.

The mechanism of action understanding, based on the mirror neuron mechanism, is conceptually similar to the proposal for how action understanding takes place according to phenomenologists, and Merleau-Ponty in particular [13]. For example, the description by Merleau-Ponty of what it means to understand an action ('The sense of gesture is not given, but understood, that is recaptured by an act of the spectator's part'; [13], p. 185), expresses nicely the direct experiential understanding of the observed actions mediated by the mirror mechanism.

It is important to stress here that, in the present review, we discuss only how the meaning of action is understood and not how the intention of the action's agent is captured. Although we are inclined to believe that simulation probably underlies intention understanding (see [14–21]) too, this issue is outside the aim of the present review.

Emotion understanding

So far, we have discussed the neural mechanism underlying action understanding. Does a similar mechanism mediate our understanding of the emotions of others? In the next sections we will show that a similar mechanism is also involved in our capacity to *understand* and *experience* the emotional states of others. We will focus on the emotion of disgust, for which rich empirical evidence has recently been acquired. We will discuss in particular the role of the insula that appears to play a fundamental role in the feeling and understanding of this basic emotion (see Box 1).

The insula and the emotion of disgust: monkey data

The insula is a heterogeneous structure. In the monkey, it can be subdivided into three cytoarchitectonic zones (agranular, dysgranular, and granular insula) [22]. Anatomical connections of the insula [23,24] reveal two main functional subdivisions: an anterior 'visceral' sector (agranular and anterior dysgranular insula) and a multimodal posterior one (posterior dysgranular and granular insula).

The anterior sector receives rich connections from olfactory and gustatory centers, a finding confirmed by functional data ([25,26]; see also [27] for a review). The anterior part of the insula also receives information from the anterior sectors of the ventral bank of the superior temporal sulcus where there are neurons that respond to the sight of faces [28–30].

Recently, it has been shown that the insula is the main recipient of interoceptive afferents. This input, after a relay in the spinal chord and the nucleus of the solitary tract, reaches specific sectors of the ventrobasal thalamic complex. These sectors project in a topographic fashion to the insula, including its gustatory sector [31]. Thus, the insula appears to be the primary cortical area not only for chemical exteroception (e.g. olfaction and taste), but also for the interoceptive state of the body ('body state representation', see [31]).

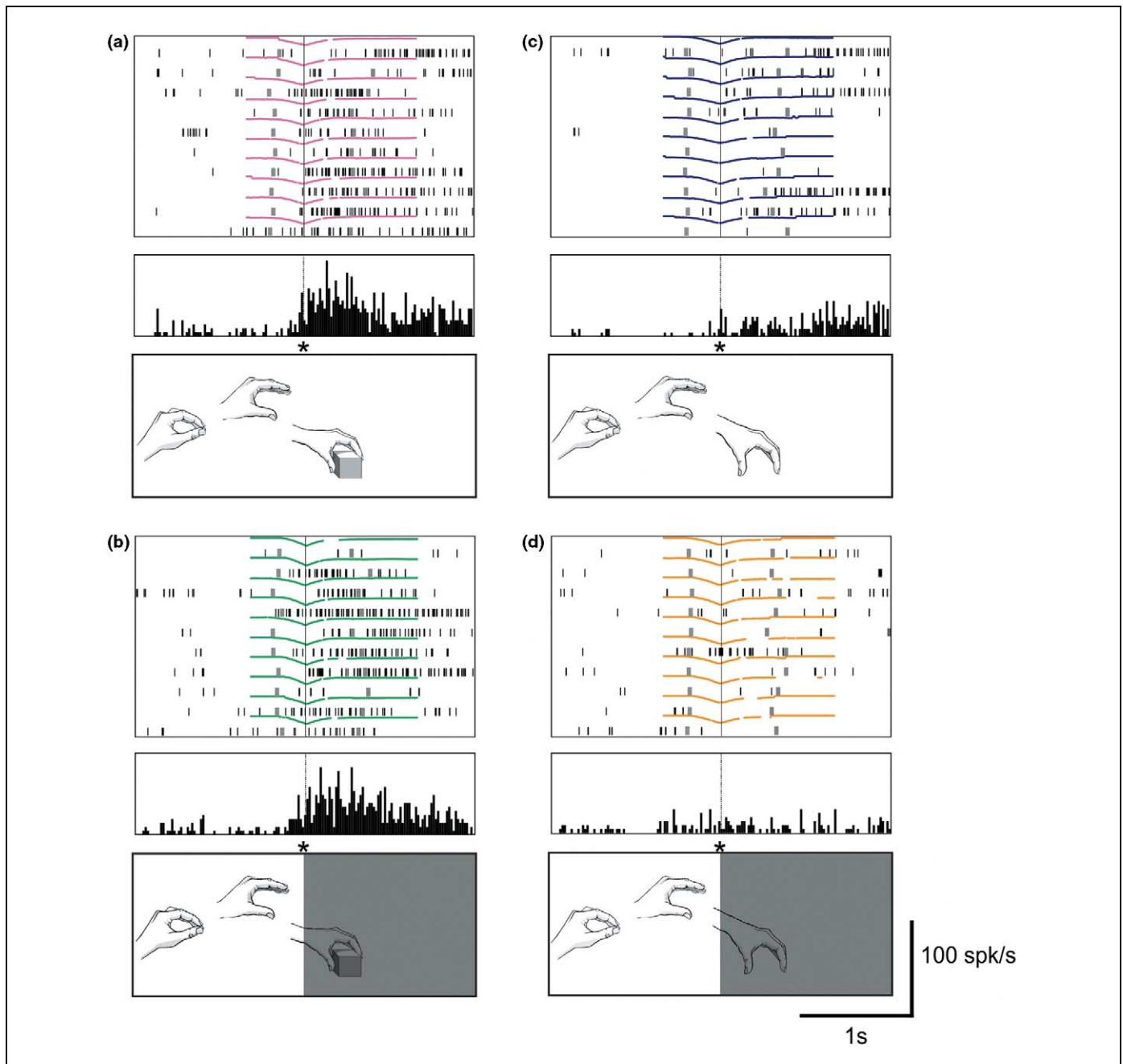


Figure 1. Example of a monkey F5 mirror neuron responding to action observation in full vision (a) and hidden (b) conditions. The lower part of each panel illustrates the experimenter's action as observed from the monkey's vantage point: the experimenter's hand starting from a fixed position, moving toward an object and grasping it (a,b), or mimicking grasping, also either in full vision (c) or hidden conditions (d). In these last two conditions the monkey observed the same movements as in (a) and (b), but without the target object. The gray square on the right in (b) and (d) represents the opaque sliding screen that prevented the monkey from seeing the experimenter's action performed behind it. A metallic frame was interposed between experimenter and monkey in all conditions. The asterisk indicates the location of a marker on this frame. In hidden conditions (b,d), the experimenter's hand started disappearing from the monkey's vision when crossing the marker position. The upper part of each panel shows raster displays and histograms of ten consecutive trials recorded during the experimenter's hand movement. Above each raster, kinematic recordings (colored traces) of the experimenter's hand are shown. The illustrated neuron responded to the observation of grasping and holding in full vision (a) and in the hidden condition (b). However, the neuron response was virtually absent in the two conditions in which the observed action was mimed (c,d). Histograms bin width $1/420$ ms. Ordinates: spikes \cdot s $^{-1}$; Abscissae: time. Reproduced with permission from [5].

Electrical stimulation of the insula of the monkey produces movements of different body parts. Unlike the responses evoked by stimulation of the classical motor areas, the movements evoked by stimulation of the insula are accompanied by a variety of autonomic and visceromotor responses [32–34]. Thus, the insula and in particular its anterior part is not only a map of the body, but also a center of visceromotor integration.

The insula and the emotion of disgust: human data
The human insula is substantially larger than the macaque counterpart, but its general architectonic organization is strikingly similar to that of the monkey and shows the same subdivisions [22]. In accord with monkey data, several brain imaging studies have shown activation of the anterior insula in response to gustatory [35,36] and olfactory stimuli [37,38]. Disgusting olfactory stimuli have been particularly studied. The observed activations were

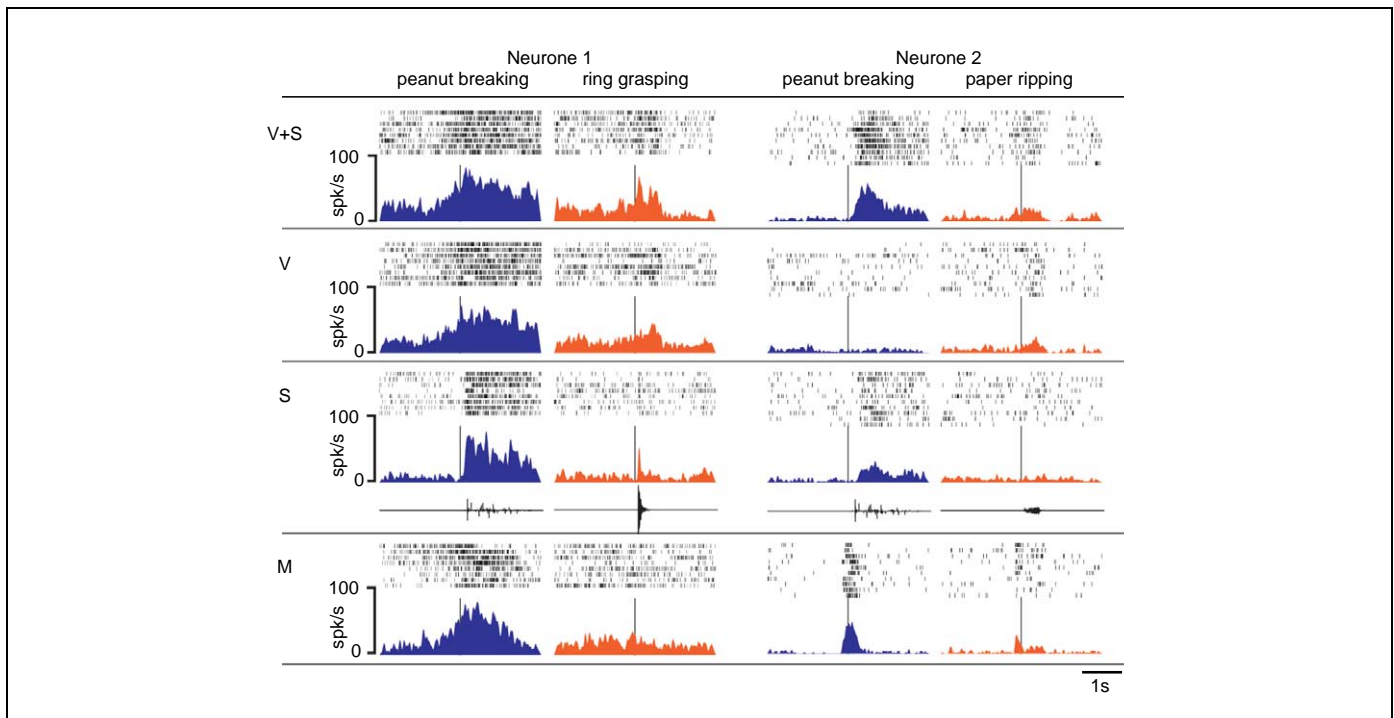


Figure 2. Responses of two neurons selectively activated by action-related sounds (e.g. breaking peanuts, ripping paper). Responses to two different actions for each neuron are shown, with the action triggering the most activation in blue. V + S, vision plus sound condition; V, vision-only condition; S, sound-only condition; M, motor condition, in which the monkey touched the object. The vertical black lines indicate either the time when the sound would have occurred (V) or the moment the monkey touched the object (M). Traces under the spike-density functions in the sound-only conditions are oscillograms of the sounds played back. Modified with permission from [6].

often found to be stronger in the left insula [37–46]. Small *et al.*, [36] showed that the left anterior insula is selective for disgusting stimuli independently of their intensity.

Most interestingly, several other brain imaging studies have shown that the anterior insula is activated by the sight of the disgusted facial expressions of others [47–50]. Phillips *et al.* [47] parametrically manipulated how disgusted the facial expressions looked, and showed that the amplitude of the insular response depended on how disgusted the observed facial expression was. These

findings were corroborated by Krolak-Salmon *et al.* [51] using depth electrode recordings in the insula of epileptic patients. They found that the electrodes located in the anterior, but not those located in the posterior insula, were selectively activated by the sight of disgusted facial expressions (Figure 3, filled green circles).

As in the monkey, electrical stimulation of the insula produces visceromotor reactions. Electrical stimulations of humans undergoing neurosurgery were performed by Penfield and Faulk [52]. Following stimulation of the anterior insula, patients reported feeling nauseous and sick. More recently, Krolak-Salmon *et al.* [51], using weaker stimulation parameters, evoked unpleasant sensations in the throat and mouth. These findings support the link between the insula and the experience of disgust and related aversive visceral sensations, and visceromotor reactions.

Clinical studies suggest an important role of the left insula in the recognition of the facial expression of disgust. Calder *et al.* [53] reported the case of the patient NK, who after lesions of the left insula and neighboring structures (Figure 3, region outlined in blue) was selectively impaired in recognizing disgust in the facial expressions of others. His recognition of the facial expression of other emotions was unaltered. This incapacity to perceive disgust extended to the auditory modality: he did not recognize the emotional valence of sounds typical for disgust such as retching, but easily recognized that of sounds characteristic of other emotions, such as laughter. This ‘disgust deafness’ extended to prosody.

Interestingly, this multimodal perceptual deficit for disgust was mirrored by an equivalent deficit in NK’s first-person experience of the same emotion: he reported

Box 1. Amygdala, insula, and selectivity for particular emotions

In this review we focus on the role played by the insula in the perception and experience of disgust. Many authors have emphasized a major role played by the amygdala in the perception and experience of fear (e.g. [64]). Phillips *et al.* [47] found activations of amygdala as well as of the insula to fearful versus neutral faces, and of the insula but not of the amygdala for disgusted versus neutral facial expressions. Zald [46] reviewed the functional imaging literature on the amygdala and showed that although fearful facial expressions are the most robust elicitors of amygdala activation, other facial expressions, including disgust, often also activate it. This last finding was not confirmed by our data [55]. This controversy is probably due to the fact that the amygdala is a complex structure, containing medial nuclei that are involved in ofactory processing, and lateral nuclei that appear more selectively involved in the visual and auditory processing of threat [65]. Given the susceptibility artifacts encountered in fMRI and the spatial limits of PET, it is difficult, if not hopeless, to differentiate these nuclei, especially if data comes from different studies. In our opinion, the present evidence suggests that the visual sectors of the amygdala are predominantly linked to the experience and perception of fear, and the anterior sector of the insula to the experience and perception of disgust.

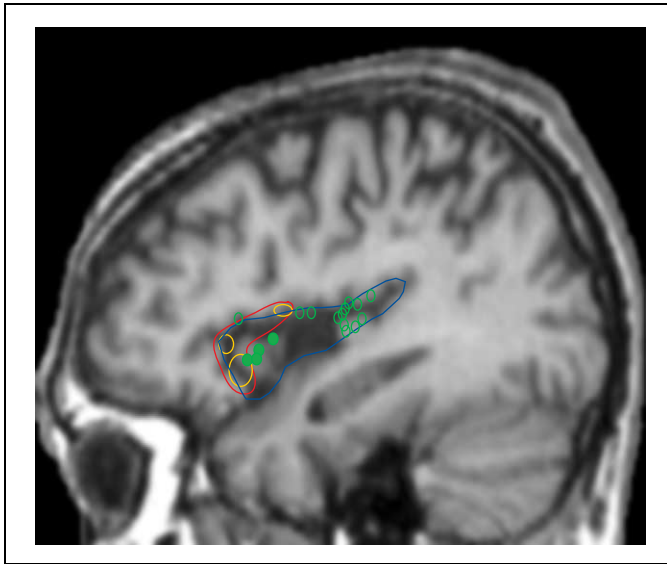


Figure 3. Sagittal T1-weighted anatomical MRI ($x = -36$) of patient NK [53] normalized to MNI space. The blue outline marks the zone of the left insular infarction. The red outline shows the zone we found to be activated during the experience of disgust; the yellow outline indicates those zones found to be common to this experience and the observation of someone else's facial expression of disgust [55]. The approximate location of the depth-electrodes of Krolak-Salmon *et al.* [51] are shown in green. Filled circles mark electrodes that showed selective responses to the sight of disgusted facial expressions.

having a blunted and reduced sensation of disgust, and ranked almost two standard deviations below the normal score in a questionnaire measuring the emotional experience of disgust. However, his experience of fear and anger were well within the normal range.

A similar pattern of deficits was reported by Adolphs *et al.* [54]. They described the patient B. who, following bilateral damage to the insula, showed substantial deficits in recognizing the facial expression of disgust, but had preserved recognition of other facial expressions. To test the hypothesis that this disgust deficit was multimodal, the experimenter acted out a dramatic display of disgust in front of the patient. "These included eating, and then regurgitating and spitting out of food, accompanied by retching sounds and facial expressions of disgust (...). B. remained entirely unable to recognize disgust, instead indicating that the food was 'delicious'", [54], p. 66. Patient B.'s incapacity to experience disgust is also evident from the fact that he ingests food indiscriminately, including inedible items, and fails to feel disgust when presented with stimuli representing disgusting food items.

Taken together, these findings raise the question of whether the same sector of the insula is involved in experiencing disgust and recognizing it in others. Strong evidence in favor of this hypothesis has recently been provided by an fMRI study. Wicker *et al.* [55] exposed participants to disgusting odorants and showed them short movie clips of other individuals smelling the content of a glass and displaying a facial expression of disgust. These activations were contrasted with those obtained when subjects were exposed to pleasant odorants or viewed the pleased facial expression of others. It was found that the anterior insula was selectively activated by the exposure to the disgusting odorants (Figure 3, region outlined in red). Most interestingly, precisely the *same*

sector within the anterior insula was activated by the mere observation of the facial expression of disgust of others (Figure 3, region outlined in yellow). Thus, it is likely that the insula contains neural populations active both when the participants directly experienced disgust and when they understood it through the facial expression of others.

These data are in accord with a previous experiment by Carr *et al.* [56], who showed activation in the anterior insula during both the observation and the imitation of facial expressions of basic emotions.

Towards a unifying neural hypothesis of the basis of social cognition

The human brain is endowed with structures that are active both during the first- and third-person experience of actions and emotions. When we witness someone else's action, we activate a network of parietal and premotor areas that is also active while we perform similar actions. When we witness the disgusted facial expressions of someone else, we activate that part of our insula that is also active when we experience disgust. Thus, the understanding of basic aspects of social cognition depends on activation of neural structures normally involved in our own personally experienced actions or emotions. By means of this activation, a bridge is created between others and ourselves.

With this mechanism we do not just 'see' or 'hear' an action or an emotion. Side by side with the sensory description of the observed social stimuli, internal representations of the state associated with these actions or emotions are evoked in the observer, 'as if' they were performing a similar action or experiencing a similar emotion.

This view on the understanding of emotions is similar to that proposed by Damasio and co-workers [57–59]. According to them, the feeling of emotions depends on the activation of the somatosensory cortices in the broader sense, and of the insula in particular. This view differs, however, from the 'as if' view we are proposing here, as far as the underlying neural mechanism is concerned. According to our view, crucial for both first- and third-person comprehension of social behavior is the activation of the cortical motor or visceromotor centers, the outcome of which, when activating downstream centers, determines a specific 'behavior', be it an action or an emotional state. When only the cortical centers, decoupled from their peripheral effects, are active, the observed actions or emotions are 'simulated' and thereby understood.

The problem of which mechanisms mediate the distinction between 'who' is really acting or first feeling an emotion when an individual is observing others' actions or emotions has been addressed by several authors. This issue is outside the scope of the present review and will be not dealt with here. For a recent review, see [60].

Besides the insula, other neural structures that appear to be involved both in the experience and perception of disgust, include the anterior cingulate cortex (ACC) and the basal ganglia (see Box 2 for this and other questions for future research). The role of these structures in emotion understanding has not been discussed here for

Box 2. Questions for future research

- Is the direct mechanism for action understanding unique to primates, or is it also present in other social animals?
- Is the capacity to understand the intentions underlying others' behavior based on mirror neurons?
- Is the direct mechanism for emotion understanding present in all mammalian species?
- Are positive emotions (e.g. happiness) understood by the same direct mechanism outlined here for negative emotions?
- What is the specific role played by anterior cingulate cortex (ACC) in understanding the negative emotions of others?
- Is the mirror system for actions and that for emotions functioning normally in people with autism, whose understanding of other minds is impaired?

the sake of space. It is important to note, however, that they are both fundamentally motor structures involved in emotion expression and action control.

Congruent with our interpretation of emotion understanding are recent data on empathy for pain [61,62]. Singer *et al.* [62], in an fMRI experiment showed that the same structures (anterior insula and ACC) that are involved in the experience and perception of disgust, also mediate empathy for pain. Considering that both anterior insula and ACC are crucially involved in pain perception and pain-related visceromotor reactions, it is likely that empathy for pain is mediated by a mechanism similar to that postulated here for disgust.

Box 3. Personal knowledge and social understanding

There is evidence that the mirror neuron system, both in monkeys [66] and humans, see [67], is not confined to the domain of transitive, object-related actions, but that it also encompasses intransitive, communicative actions. In a recent fMRI study, participants observed mouth actions performed by humans, monkeys and dogs [68]. These actions could be either transitive, object-directed actions, like a human, a monkey, or a dog biting a piece of food, or intransitive communicative actions, like human silent speech, monkey lip-smacking, and dog barking. The results showed that the observation of all biting actions led to the activation of the mirror circuit, encompassing the inferior parietal lobule and ventral premotor cortex [68]. Interestingly, the observation of communicative mouth actions led to the activation of different cortical foci, according to the different observed species (Figure 1). Actions belonging to the motor repertoire of the observer (e.g. biting and speech reading) or very closely related to it (e.g. monkey's lip-smacking) are mapped on the observer's motor system. Actions that do not belong to this repertoire (e.g. barking) are mapped and henceforth categorized on the basis of their visual properties.

This dichotomy between a direct, motor-mediated type of action understanding, and a cognitive type based on the interpretation of visual representations, is most likely also true for emotion understanding. The data reviewed here show that in the anterior insula, visual information concerning the emotions of others is directly mapped onto the same visceromotor neural structures that determine the experience of that emotion in the observer. This direct mapping can occur even when the emotion of others can only be imagined [62]. We do not maintain that the direct mapping is the only way in which the emotions of others can be understood. It is likely that others' emotions can be also understood on the basis of the cognitive elaboration of the visual aspects of their expression. We do not take these two possibilities as being mutually exclusive. The first, probably the more ancient in evolutionary terms, is experience-based, whereas the second is a cognitive description of an external state of affairs. It is likely that the direct visceromotor mechanism scaffolds the cognitive description, and, when the former mechanism is not present or malfunctioning, the latter provides only a pale, detached account of the emotions of others.

It is important to stress that we are not claiming that the understanding of emotions is solely mediated by the simulation mechanism described here (for alternative simulation models of emotion understanding, see [63]). As mentioned above, emotionally neutral actions can also be understood without eliciting their corresponding motor representation. The same might be true for emotion recognition. However, we believe that this recognition is fundamentally different from that based on simulation, because it does not generate that experiential knowledge of the observed social stimuli that the activation of visceromotor structures produces. It determines only a cognitive interpretation of them (see Box 3).

Social cognition is not only *thinking* about the contents of someone else's mind (see, [21,63]). Our brains, and those of other primates, appear to have developed a basic functional mechanism, a mirror mechanism, which gives us an experiential insight into other minds. This mechanism could provide the first unifying perspective of the neural basis of social cognition.

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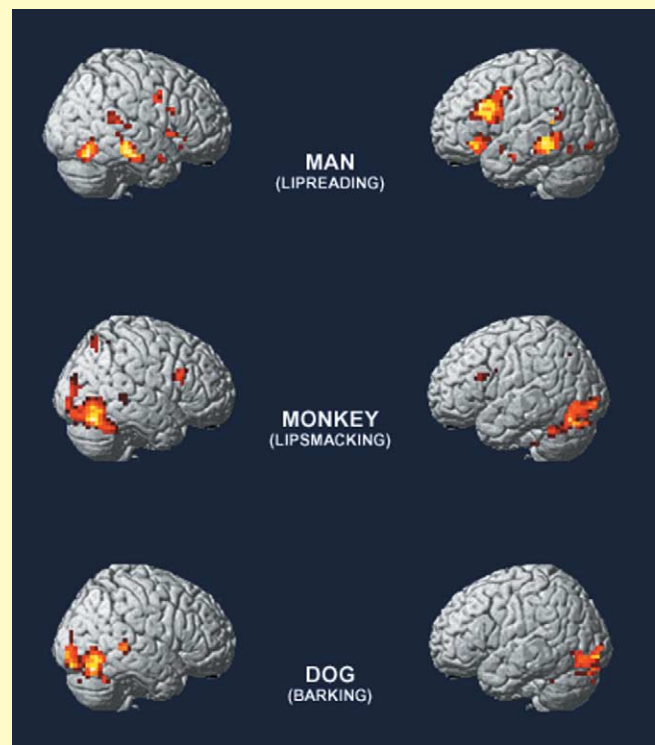


Figure 1. Cortical areas activated during the observation of oral communicative actions performed by a man (silent speech), a monkey (lip-smacking), and a dog (barking). Reproduced with permission from [68].

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