a remnant chloroplast, with an associated genome. Perhaps most notorious among these is the world's most dangerous 'alga', the malaria parasite *Plasmodium* [15]. Whether anything has gone further and lost both the chloroplast compartment and its genome is less clear, although *Cryptosporidium*, a relative of *Plasmodium*, may have done so [16].

In the mitochondrial lineage, the most plausible remaining role for mitosomes is iron-sulphur cluster biogenesis. However, in *Entamoeba*, even this biogenesis function seems to have been taken over by proteins of non-mitochondrial origin. Their location in the cell remains to be established and so the role of mitosomes in *Entamoeba* remains unclear [17]. In *Trachipleistophora hominis*, at least part of the iron-sulphur-cluster biogenesis pathway has been delegated to the cytosol [18]. So there may well be organisms where the whole of this role has been delegated by the mitochondrion, and where after over a billion years of trying to make themselves indispensable, the mitochondrion and its descendants have finally disappeared, like the grin of Alice in Wonderland's Cheshire Cat.

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Department of Biochemistry, University of Cambridge, Tennis Court Road, Cambridge CB2 1QW, UK.
E-mail: c.j.howe@bioc.cam.ac.uk

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Action Understanding: How, What and Why

The mirror neuron system may help us understand how others act and what they do. A recent study has shown that consciously reflecting on their intentions additionally recruits mentalizing areas.

Marc Thioux, Valeria Gazzola and Christian Keysers

You are a student interested in the origin of life and have an appointment with a renowned scholar in a café. When you arrive, he is already sitting at the terrace, absorbed in a book. You introduce yourself, and are invited to take a seat. The conversation goes on for an hour, then slows down. The professor leans back into his chair and reaches with his left hand for one of the books on the table. Your perception of this last action has at least three levels. At the lowest, most detailed level, you could perceive *how* he performed this action: with his left hand, using a whole hand prehension. At the intermediate level, you perceive *what* he is doing: grasping a book. At the highest level you might perceive *why* he is doing it: to signal that your conversation is over. The last decade brought major advances in our understanding of the cerebral structures involved in processing the *how*, *what*, and *why* of other people's actions. In a paper published recently in *Current Biology*, de Lange *et al.* [1] have addressed the question of how our brain flexibly switches between these various levels by comparing brain activity while people attend to the *how* or *why* of other people's actions.

Progress in this field suffered from a division into two camps [2], who have taken different views of how the neural processes underlying our understanding of what others are doing. One of the camps has taken the view that this involves a process referred to as mentalization — conscious thinking about the state of minds of other individuals [3]. Researchers in this camp have emphasised data showing that certain regions of the paracingulate gyrus are activated when subjects mentalize; Grezes *et al.* [4] and Brass *et al.* [5] suggest that such regions can provide information about 'why' other people perform certain actions.

The other camp has emphasised the importance of the 'mirror neuron system'. This view was originally stimulated by research on monkeys, in particular the discovery of single cells in the monkey's superior temporal

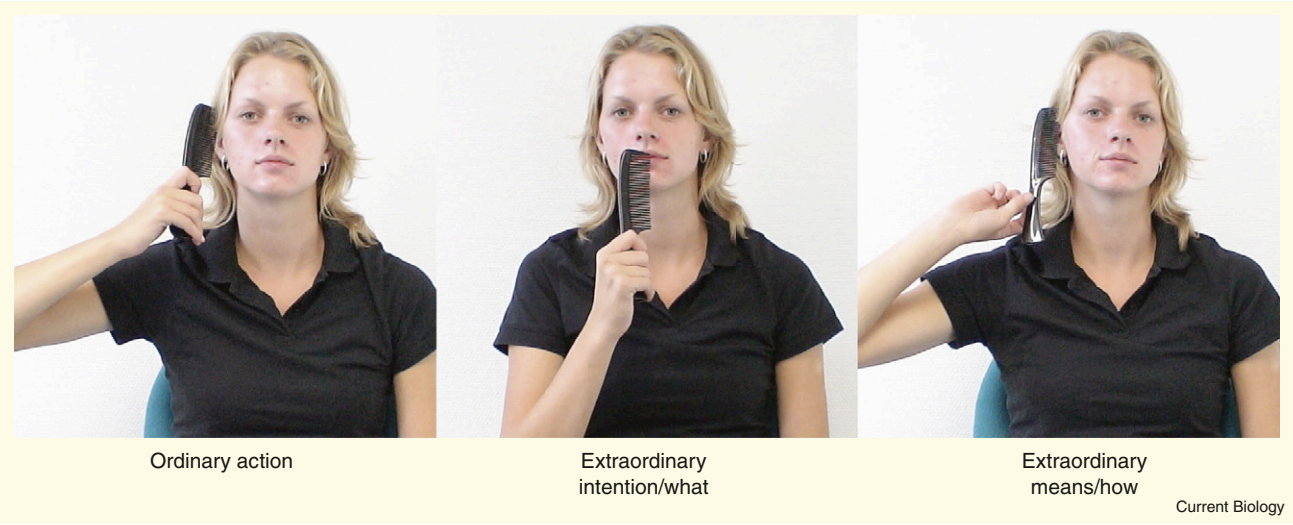

Figure 1. Example of the stimuli used by de Lange *et al.* [1].

sulcus that respond to the sound or sight of other people's actions, providing sensory descriptions of what other individuals do [6,7]. Later, mirror neurons were discovered in the monkey's premotor, and posterior parietal cortex [7–12]. Mirror neurons fire when the monkey executes an action, or when the monkey hears [10,13] or sees [8,12] other individuals perform similar actions. This suggests that the monkey has brain circuits that associate its actions with those of others, providing an 'inner sense of action' to the actions of others [12].

A minority of mirror neurons (about a third) respond only to the sight of actions that match the effective executed actions in minute detail [8], providing a direct representation of *how* the other individual performed the action. The majority, however, also respond if the monkey sees someone perform a similar action using different effectors, for example grasping with the other hand, or with the mouth [8]. Such broadly congruent mirror neurons activate various action representations that differ in motor details from the observed action but achieve the same goal and could thus convey a feeling for *what* the other person does.

Two additional lines of evidence link mirror neurons with *what* other people do. First, most mirror neurons respond to the sight of someone grasping an object, but not if the same movement is mimed without an object — two actions that do not differ in terms of 'how' the action is performed, but only in 'what' is being done [8,11]. Second, many mirror neurons also respond to the sound of actions (for example, the breaking of a peanut). Such sounds, however, are emitted by the object, and reflect *what* is being done without containing explicit information about *how* it has been done: was it broken by two hands or by the mouth? The fact that, in monkeys not engaged in any explicit task, auditory mirror neurons respond approximately 100 milliseconds after the onset of an action sound [10,13] suggests that their responses are spontaneous and stimulus-driven.

Neuroimaging studies have confirmed the presence of a similar mirror neuron system in humans [12,14–17]. Repetition suppression paradigms have shown that some regions within the mirror neuron system represent the *what* and others the *how* of other people's actions [17]. Other studies have found that the *what* appears to be dominant: viewing actions that have a familiar goal, but are executed in unfamiliar ways — for example, by a robotic arm or by an effector the observer is lacking — activates this system as strongly as actions that match both in terms of *what* and *how* [15,16]. Finally, the sound of actions, deprived of direct information about *how* the action is done, also recruits the human mirror system [14].

In constrast to investigators who have considered mentalizing or mirroring as competing accounts of how we perceive other people's actions [18], we have suggested that these systems might integrate: in particular, that mirror systems translate perceived actions into motor (and somatosensory [14,15,19]) representations of *how* and *what* others do. These simulated representations can later be interrogated by more deliberate mentalizing systems to reflect on *why* other people acted [2]. De Lange *et al.*'s [1] study now sheds further light onto this relationship.

They presented their participants with pictures of familiar actions such as combing your hair. They compared these images with images in which either the *how* or *what* was extraordinary (Figure 1). They found that varying *how* the action was performed had the strongest effect in high-level visual areas. In regions traditionally associated with the mirror neuron system, this manipulation only had weak effects. In contrast, changing *what* was done had the strongest effect in the inferior frontal gyrus often associated with the mirror neuron system.

Comparing these inferior frontal gyrus clusters with the regions of the brain that show activity while participants observed and executed similar hand actions in another experiment [15] — for example, bringing a glass to the mouth — shows that these inferior frontal gyrus clusters were close to, but probably not within, the mirror neuron system (Figure 2). In the future, it will therefore be important

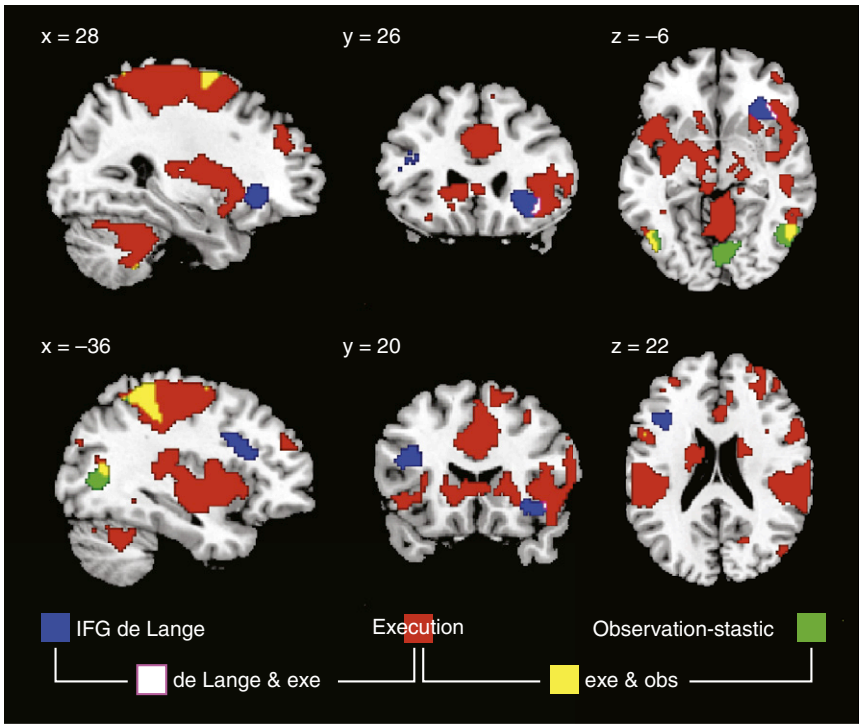

Figure 2. Two inferior frontal gyrus clusters shown by de Lange *et al.* [1] to respond more to actions with extraordinary intentions (blue) together with regions involved in the observation of movies or the execution of similar actions from another experiment [15].

to examine a similar experimental paradigm while including a motor execution task in the same participants.

Interestingly, whether participants were asked to decide if the means or the intentions of the actions were extraordinary had little effect on the activity in the inferior frontal gyrus, suggesting that the inferior frontal gyrus activity was more stimulus than task driven. In contrast, regions traditionally associated with mentalizing, such as the paracingulate gyrus, were strongly affected by the task. As participants examined *how* the action was performed, these regions were inhibited relative to rest and did not differentiate between ordinary and extraordinary actions, but when participants paid attention to people's intentions, they were more active (albeit still less than rest) and differentiated between actions. This supports the idea that mentalizing regions *can* analyze other people's actions but only if the viewer decides to reflect upon their goals, intentions and beliefs [2]. The pattern of response in these areas leaves a key question for future experiments: what computations on actions take place in these areas?

The new work of de Lange *et al.* [1] has thus finally shown that brain regions involved in mentalizing, and those close to the mirror neuron system, *can* work in concert in the brain, but do so only if participants deliberately reflect on goals and intentions. In addition, a large body of evidence suggests that high level visual areas and the mirror neuron system process *how* [8,12,17] and *what* [7–11,13–17,20] others do even without explicit mentalizing [14–16]. Does this suggest that there is a division of labour with mentalizing areas processing *why* people act, the mirror neuron system *what* they do, and visual areas *how* they do it? Probably not. In the opening example, understanding that the professor reached for the book to end the conversation presupposes a processing of *what* and *how* he does it. For understanding *why*, visual areas and regions of the mirror neuron system computing *how* and *what* are likely to be as important as mentalizing areas. Also splitting *how* and *what* between visual areas and mirror neuron system is artificial: all mirror neurons need visual input and different mirror neurons represent both *how* and *what* [12,15,16].

What this study [1] does show is that our action perception system is highly integrated, spanning the inferior frontal gyrus associated with the mirror neuron system and areas associated with mentalizing [2]. What we try to find out about other people's actions, however, determines how and where in the brain processing takes place. Hopefully this finding will shift people's attention away from fruitless discussions about whether mirroring or mentalizing is the basis of social cognition, towards the more interesting and still unanswered question of what neural computations are involved when we mentalize about actions we mirror.

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University Medical Center Groningen, University of Groningen A. Deusinglaan 2, 9713AW Groningen, The Netherlands.
E-mail: c.m.keysers@rug.nl

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