# Mirror neurons or emulator neurons?

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*Mirror neurons are cells in the macaque brain that discharge both when the monkey performs a certain action and when it observes someone else performing similar actions. It has been suggested that the main function of these neurons is to make the goal of the observed actions understood by internal simulation. I propose that the function of these neurons is different: predictive emulation, rather than postdictive mirroring, of observed actions.*

The discovery of mirror neurons (MNs) in monkeys, and the mirror neuron system in humans, has been hailed as the most important finding of the last decade in neuroscience (Ramachandran, 2000). These cells are primarily located in the ventral premotor area of F5 of the macaque brain and have both motor and visual properties (di Pellegrino et al., 1992; Jeannerod et al., 1995; Gallese et al., 1996; Rizzolatti et al., 1996; Ferrari et al, 2005). They discharge when the monkey executes specific goal-directed hand or mouth actions, and they are also activated when the animal observes another individual performing similar actions. Neurons with comparable mirror properties have also been discovered in the inferior parietal lobule (Gallese et al., 2002; Fogassi et al., 2005). Certain areas of the human ventral premotor and posterior parietal cortex have been shown to be activated by executing, observing, or imitating goal-directed actions in neuroimaging studies (Rizzolatti & Craighero, 2004), and are thought to form a mirror neuron system in humans.

Mirror neurons have been suggested to be the key element in the explanation of diverse phenomena from the evolution of language (Rizzolatti & Arbib, 1998), through imitation (Iacoboni et al., 1999; Iacoboni, 2005) and intersubjectivity (Gallese, 2003), to empathy (Iacoboni, 2005) and autism (Oberman et al., 2005). However, the immediate and evolutionary more ancient function that these neurons serve is thought to be simpler: they help to understand observed actions by extracting and representing the goal, or the meaning, of those actions (Rizzolatti et al., 2001; Rizzolatti & Craighero, 2004). This suggestion, also known as the *direct-matching hypothesis* (Rizzolatti et al., 2001), attempts to solve the thorny question of how we, and other primates, go beyond the perceptual information about the observed behaviour of our conspecifics to get a deeper understanding of why they act the ways they do. According to this hypothesis, "an action is understood when its observation causes the motor system of the observer to 'resonate'" (Rizzolatti et al., 2001, p. 661), and this resonation allows the observer to figure out the outcome, and ultimately the goal, of the action because "he know[s] its outcomes when he does it" (Gallese et al., 2004, p. 396).

In fact, it seems to be "generally accepted that the fundamental role of mirror neurons is to allow the observing individual to understand the goal of the observed motor act" (Fogassi et al., 2005, p. 665), or in other words, that MN activation leads to goal understanding in the observer (Blakemore & Frith, 2005). Here I shall attempt to show that the empirical evidence from single-cell studies in monkeys and from human neuroimaging is not consistent with this generally accepted interpretation of mirror neuron function, but it is compatible with the opposite causal sequence, i. e., that goal understanding leads to MN activation. If this is correct then MNs serve a different, but not less important, function from what is usually attributed to them: action prediction by emulation.

**Actions and goals**

The term 'action' usually refers to behaviours that are interpreted in functional terms, i.e., in relation to goal states. Because the relationship between actions and goals (or means and ends) is systematic (non-random), information about either of them can be used to get information about the other one. Thus, one can posit two different computational systems: one that receives information about an action and outputs a goal for it (*action-to-goal*), and another one which generates an appropriate action for the goal appearing at its input (*goal-to-action*). The same contrast between the two kinds of computation has also been formulated at various fields in behavioural and neurosciences (see Table 1). Simulation theories of mindreading (Gallese & Goldman, 1998) postulate two kinds of simulation: *predictive* simulation, which finds a likely action for a known goal by pretending that the observer has the same goal ("What would I do if I had the same goal?"), and *postdictive* (or *retrodictive*) simulation, which extracts, similarly by pretence, mental states that produced an observed action ("What goal would make me do this?"). Theories of animal social learning have also developed a similar distinction. *Imitative* learning concentrates to the means, and acquiring the means action leads the animal to get to the goal. In contrast, in learning by *emulation* the individual discovers a desirable goal state that can be achieved in a situation, and generates its own actions that lead to the goal. Theories of motor control also postulate two kinds of internal models that connect motor commands and end states (Wolpert & Ghahramani, 2000). The *forward model* (predictor) receives an efferent copy of the motor command and generates the expected sensory outcome for it, while the *inverse model* (controller) produces the motor commands that are appropriate to accomplish a desired end state.

| Computation | Action to Goal | Goal to Action |
|---|---|---|
| Simulation | Postdictive | Predictive |
| Learning | Imitation | Emulation |
| Motor Control | Forward Model | Inverse Model |

**Table 1**

**Understanding goals by mirror neurons**

How does the motor system help to understand the goal of observed actions? The motor function of the neurons in area F5 of the premotor cortex is to provide a 'motor vocabulary' for the execution of goal-directed actions, and to perform visuomotor transformation between visually defined goal-states and the motor system (Rizzolatti et al., 1988; Jeannerod et al., 1995). This is essentially a *goal-to-action* type of computation, roughly corresponding to the internal 'inverse model' posited by computational theories of motor control (Wolpert & Ghahramani, 2000). Interestingly, the function that the direct-matching hypothesis assigns to mirror neurons requires an opposite, *action-to-goal* computation. The input to this computation is provided by the copy of the motor command for the observed action generated by the automatic resonation upon action observation and its result is the likely goal for the observed action.

How would these two opposite functions (goal-to-action and action-to-goal computations) fit into a single neural system? One answer to this question was suggested by Blakemore and Decety (2001), who proposed that, in case of action observation, the direction of information flow would be reversed in the motor system, allowing the observer to infer backwards from the sensory outcome to the motor command, and from the motor command to the intention that preceded the action. However, this solution is unlikely to be feasible, not just because the difficulties and inefficiency of reversing information flow in a computational system, but also because of the high degree of freedom of solving such an inverse problem (the same motor command can be the result of a wide variety of intentions, see Jacob & Jeannerod, 2005).

A more plausible proposal is that action observation exploits another element of the motor control loop, the internal 'forward model' (Miall, 2003; Iacoboni, 2005). If the mirror system replicates the motor command that corresponds to the motor output that has produced the observed action, it can be fed into the observer's forward model whose function is to generate the likely sensory outcome of the motor command (see Fig. 1a). Since the outcome of a motor act normally matches the goal that generated the action, such a mechanism would indeed result in an understanding of the goal of an observed action. For example, when the monkey watches someone reach for an object, its 'forward model' will anticipate the sensory feeling that grasping the object would produce, and this identifies the goal of the observed action.

## Predicting actions by mirror neurons

An alternative proposal for the function of mirror neurons is that their job is monitoring, anticipating, and predicting other individuals' oncoming actions, rather than reproducing them in order to understand them (Prinz, in press; Wilson & Knoblich, 2005). Perception of dynamic events, whether or not they involve social stimuli, is always predictive in nature (Wilson & Knoblich, 2005) and the human ventral premotor cortex plays an important role in anticipating oncoming events (Schubbotz & von Cramon, 2004). The obvious advantage of 'being ahead' of events is that it gives the perceiver the opportunity to interfere in time and allows for the quick recruitment of resources to deal with unexpected events. When observing conspecifics, one way to anticipate their behaviour is to hypothesize their goals they pursue and to make action predictions with the help of the observer's own motor system.

Under this interpretation, mirror neurons perform the same type of (goal-to-action) computation during action observation as they do during action execution. In terms of a simple motor loop (see Fig. 1b), the mirror system works by receiving a 'goal' as an input and producing an action as the output, but here the 'goal' is the hypothesized goal of the observed individual, computed outside the motor system, and the 'action' is the prediction generated for its next move. In other words, the motor system is used here as a simulation (or 'emulation') device (Grush, in press), but this is predictive rather than postdictive simulation (Wilson & Knoblich, 2005). For example, when the monkey watches someone reach for an object, it generates hypotheses about the likely goal of that action (e.g., grasping, or eating, it), and can use its own inverse motor models to predictively simulate the subsequent acts the other would perform (e.g., putting food into the mouth).

## Contrasting MN functions

The main difference between the two interpretations of mirror neuron function is that while the 'goal-to-action' account (Fig. 1b) explains the reproduction of observed actions by the inverse model (or 'controller' see also Wolpert et al., 2001), the 'action-to-goal' account (Fig. 1a) postulates a new entry point to the motor loop during action observation. This new entry point is the mirror system, which duplicates the motor command necessary for the observed action by 'direct matching', bypassing the normal route through the motor controller (the inverse model).

In the following, I shall highlight five aspects the empirical evidence on mirror neuron activation in monkeys, and ventral premotor activation in humans, that are not consistent, or even in conflict, with the goal-understanding function, while they are compatible with the action-prediction function, of this neural system.

### 1 No MN activation without a goal

Mirror neurons do not respond to mimicked actions, for example, when the monkey observes the experimenter pretending to grasp something in the absence of any objects (Gallese et al., 1996). MNs remain silent in this situation not because they need to see the target object of an action, since they discharge when the experimenter reaches behind a barrier where the monkey knows there is a piece of food (Umiltà et al., 2001). MNs are not activated by mimicked actions because they are only interested in meaningful, goal-directed actions (Rizzolatti et al., 2001). Similar phenomena were also demonstrated in human neuroimaging studies. Although the human ventral premotor cortex is sometimes activated by the observation of intransitive actions (Iacoboni et al., 1999), the activation is higher for goal-directed actions than for actions whose the goal is not evident (Nishitani & Hari, 2000; Chaminade et al., 2002; Koski et al., 2002; Johnson-Frey et al., 2003).

This aspect of MN activation has been regarded as indicating that MNs actually represent the goal of the action, and as evidence that they perform an action-to-goal computation. However, if MN activation represents the goal, what is the evidence that this goal is derived from action reproduction? In other words, if MN activation is not evidence for automatic mirroring, but for goal extraction by the forward models, then how do we know that the goal, represented by MNs, is extracted from motor mirroring? Conversely, if MNs represent mirroring and are activated only by goal-directed actions, then some other process must have figured out beforehand whether an observed action is to be mirrored or not, and that process has already recognized whether the action is goal-directed or not. Clearly, the problem here is that mirror neurons cannot perform their own input (action mirroring) and output (goal extraction) function at the same time.

In contrast, the fact that MNs are activated only by goal-directed actions is completely consistent with the goal-to-action account of mirror neuron function. Mirror neurons respond only to meaningful actions because only the meaning, or the assumed goal, provides input to the motor loop (Fig. 1b) and enables action predictions. It is worth noting that mirror neurons do not passively reflect observed actions but seem to anticipate them (Gallese et al., 1996). 'Grasping mirror neurons', for example, start to discharge hundreds of milliseconds before the observed hand touches the target object, as if they mirrored the future. When observing actions, humans also anticipate the next move of the observed individual, and this is evident in their eye movement patterns (Flanagan & Johansson, 2003), as well as in the motor (Kilner et al., 2004) and ventral premotor cortex (Nishitani & Hari, 2000; Ramnani & Miall, 2004) activation. In all these cases, the observer's own motor activation was triggered by their understanding of the goal, or immediate subgoal, of the observed individual, and simulated predictively what the other should do to achieve that goal.

### 2 MN response reflects further goals

The activation of mirror neurons depends not only on the presence of goals, but may also be tailored to the further, or higher level, goals of the observed individual. In a recent study, Fogassi et al. (2005) trained monkeys to perform two actions: grasping an object and putting it into their mouth (i.e., eating it), or grasping an object and putting it into a container (placing). Although the first part of these actions (grasping) was the same and kinematically indistinguishable, the researchers found separate sets of mirror neurons in the inferior parietal lobule, which were preferentially activated before and during grasping according to the subsequent, to-be-executed action. In other words, some MNs showed higher activation when the monkey grasped the object to eat it, while others were more active when the monkey was about to place the object into the container. Crucially, these neurons responded similarly when the monkey observed the same actions performed by an experimenter. When the experimenter was about to eat the object, the 'grasping to eat' neurons were selectively activated; when he was about to place the object into the container, the other set of mirror neurons fired. This is a clear demonstration that mirror neurons take into account the further goal, and not just the perceived action, when responding to observed actions.

A neuroimaging study has recently concluded that the human inferior frontal cortex behaves the same way during action observation. Iacoboni et al. (2005) presented observers with actions (grasping a cup) either out of context, or in contexts that indicated one of two underlying intentions ('drinking tea' or 'cleaning up'). BOLD activation in the right inferior frontal cortex was higher when the context indicated the intention, i.e., the further goal, than when the action was presented alone, and the authors also found evidence for differential activation for the two intentions within the same region.

It is hard to see how action reproduction by mirroring would explain the differential activations in these studies, because there was no way to figure out the intention of the actor from the action alone. The researchers in both studies made sure that, whatever the intention in the observed action would have been, the perceptual and motor properties of the initial action (grasping) were the same, and so its reproduction could not reveal the further goal. Thus, these findings cannot be explained by engagement in action-to-goal computation, or by activating forward motor models to generate expected outcomes.

In contrast, these results fit perfectly with the goal-to-action account of mirror neuron activation. Although the actions themselves did not carry information about the further goal of the actor in the studies cited above, the context did. For example, the monkey in the Fogassi et al. (2005) study could figure out the further goal of the observed action from the kind of object (food or non-food) involved, and whether or not a container was present. Such a goal attribution allowed them to make predictions, using their own inverse model, about the subsequent actions of the actor, and this explains the differential activation of mirror neurons during the observation of the initial action, which itself was not different between experimental conditions.

## 3 Irrelevant goals

Mirror neurons are not, or only very weakly, activated by actions observed on video monitors (Ferrari et al., 2003; Keysers & Perrett, 2004). MNs do not respond to observed actions even with 3D, stereoscopic presentation. MNs have also been claimed to be unselective to the significance of target object of the action, especially whether it is a piece of food or a geometric solid (Rizzolatti & Craighero, 2004). Nevertheless, while MNs always discharge to food-related actions, the response diminishes or disappears "after a few or even the first presentation" (Gallese et al., 1996, p. 605) to non-food objects. Thus actions, which are not relevant to the monkey, are less likely to activate mirror neurons. An analogous effect in human neuroimaging is that action observation activates the ventral premotor cortex more when the observed action is to be imitated later than when it has no further relevance (Buccino et al., 2004).

If mirror neurons perform action-to-goal computations, lack of MN activation would imply that the monkey has not understood the goal of the action seen on video monitors. However, activation patterns of neurons in the superior temporal sulcus (STS), which do not have motor properties, suggest that monkeys give fairly high-level interpretation to actions observed on video (e.g., Jellema et al., 2000; Jellema & Perrett, 2003; Barraclough et al., 2005) and are not blind to their meaning. Also, the goal of the action does not change with repeated presentation, and automatic mirror neuron activation should find it, whether or not it involves food. It is not clear how the action-to-goal view of mirror neuron function would account for modulation of MN activation by goal relevance, which itself requires prior goal-extraction.

These facts could easily fit into the goal-to-action account though. Neurons in the premotor F5 area are known to be sensitive only to "motivationally meaningful stimuli" (Rizzolatti et al., 1988). An action whose outcome is irrelevant to monkey either because its goal does not involve food or because it is executed in another, inaccessible world behind the video screen, is not worth monitoring. The more important the goal of an action, the more important to predictively track its execution. As the above findings suggest, the evaluation of relevance, hence the extracting the goal, of an action precedes rather than follows mirror neuron activation, which is consistent with the goal-to-action view of mirror neuron functioning.

## 4 Canonical and mirror neurons

Canonical neurons are cells in close proximity to mirror neurons in the F5 area of the premotor cortex (Murata et al., 1997). Just like mirror neurons, they are active whenever the monkey grasps objects, and their activation is specific to the type of grip the monkey executes during grasping. Canonical neurons also respond to visual stimuli, but unlike mirror neurons, they are sensitive to the sight of static objects. Importantly, their visual activation is selective to the sight of the same object shape that requires the specific grip type characterizing the motor property of the neurons. The human ventral premotor cortex has also been shown to be activated by the sight of manipulable objects, like tools (Chao & Martin, 2000; Grèzes & Decety, 2002; Grèzes et al., 2003).

If mirror neurons were involved in action-to-goal computations, canonical and mirror neurons would represent two completely different classes of neurons. Canonical neurons perform visuomotor transformations – they match motor actions to object shape (Jeannerod et al., 1995) – while mirror neurons find goals to actions. In contrast, if mirror neurons perform goal-to-action computations – they match motor actions to already understood goal states – the two classes of neuron share their overall function: action generation for representation (and not necessarily execution) purposes. Both classes of neuron act as inverse models, and the main difference between them is not the computation they perform but rather the input information they rely on. While canonical neurons receive their input as a (desired) object's shape from the anterior intraparietal area (AIP, Rizzolatti et al., 2002), it is the hypothesized goal of an observed action that triggers mirror neurons.

## 5 Weak visuo-motor congruency

The main functional characteristic of mirror neurons is that they become active both when the monkey makes a particular action, and when it observes another individual making a similar action (Rizzolatti et al., 2001). What is the degree of similarity here?

About one third (19 to 41 %) of all MNs show a clear one-to-one congruence ('strict congruence') between visual and motor properties of the cells (di Pellegrino et al., 1992; Gallese et al., 1996; Gallese et al., 2002; Ferrari et al., 2003). In these neurons, the effective observed and effective motor action is the same not just in terms of overall action category (e.g., grasp) but also in terms of the way it is executed (e.g., grip type). However, a sizeable proportion (21 to 68 %) of MNs respond to not just one, but two or even more types of observed actions (di Pellegrino et al., 1992; Gallese et al., 1996; Umiltà et al., 2001; Gallese et al., 2002; Ferrari et al., 2003). For example, a neuron that is associated with the 'grasping by hand' motor action could be activated by the observation of 'hands interaction', or by 'grasping with the mouth' (Gallese et al., 1996). Even when a MN is activated only by the observation of a single action, it is not necessarily the same action as defined by the motor properties of the neuron. Examples are the so-called 'broadly congruent' mirror neurons, which make up the majority of all MNs (Fogassi & Gallese, 2002). For instance, di Pellegrino et al. (1992) reported that in 11 of the 29 MNs (38 %) the effective observed and effective executed actions were 'logically' related. "For example, the effective observed action was placing an object on the table, whereas the effective executed action was bringing food to the mouth or grasping the object" (di Pellegrino et al., 1992, p. 179). Finally, in a further 10 % of MNs no relation was found between the effective executed and observed actions (Fogassi & Gallese, 2002).

According to the action-to-goal account of mirror neuron function, the goal of an observed action is extracted from its mirrored version, which has been generated by automatic resonation, and so the accuracy of goal understanding will be at most as good as the accuracy of action reproduction in the observer's motor system. However impressive are sometimes the matching abilities shown by mirror neurons, if monkeys relied on them in understanding the goal of others, they would frequently misunderstand observed actions. The 'logically related' neuron, cited above, for example, mirrored an action (placing an object onto a surface) by another action (grasping an object from a surface) that had practically the opposite goal.

Weak visuo-motor congruence does not pose a problem for the goal-to-action account of mirror neurons (because action prediction does not require accurate matching), but, in fact, can be explained by it. Two or more kinds of observed actions, when interpreted in terms of their further goals, can lead to the same prediction, and the 'logically related' actions that have been described as examples of broad congruence between executed and observed actions may indeed reflect this kind of sequential relation. At the same time, while many neurons 'look far ahead', and predict forthcoming actions in an action sequence, some of them simply anticipate the finishing of the ongoing motor act, and appear to mirror it.

## Conclusions

Many aspects of mirror neuron activation suggest that mirror neurons are more likely to be involved in generating action predictions for goal-directed actions, where the goal has been extracted from contextual cues, than in finding goals for automatically reproduced actions. This conclusion implies that mirror neurons are indeed involved in simulation of observed actions, but this is predictive rather than postdictive simulation. Thus, mirror neurons do not provide direct support for simulation theories of mind reading (Gallese and Goldman, 1998), which require postdictive, action-to-goal simulation. The goal-to-action account of mirror neuron function also implies that mirror neurons will sometimes reproduce actions, but this is achieved by emulation rather than by automatic copying. Accordingly, since mirror neurons, despite their name, do not 'mirror' actions, the term 'emulator neuron' would describe their function more accurately.

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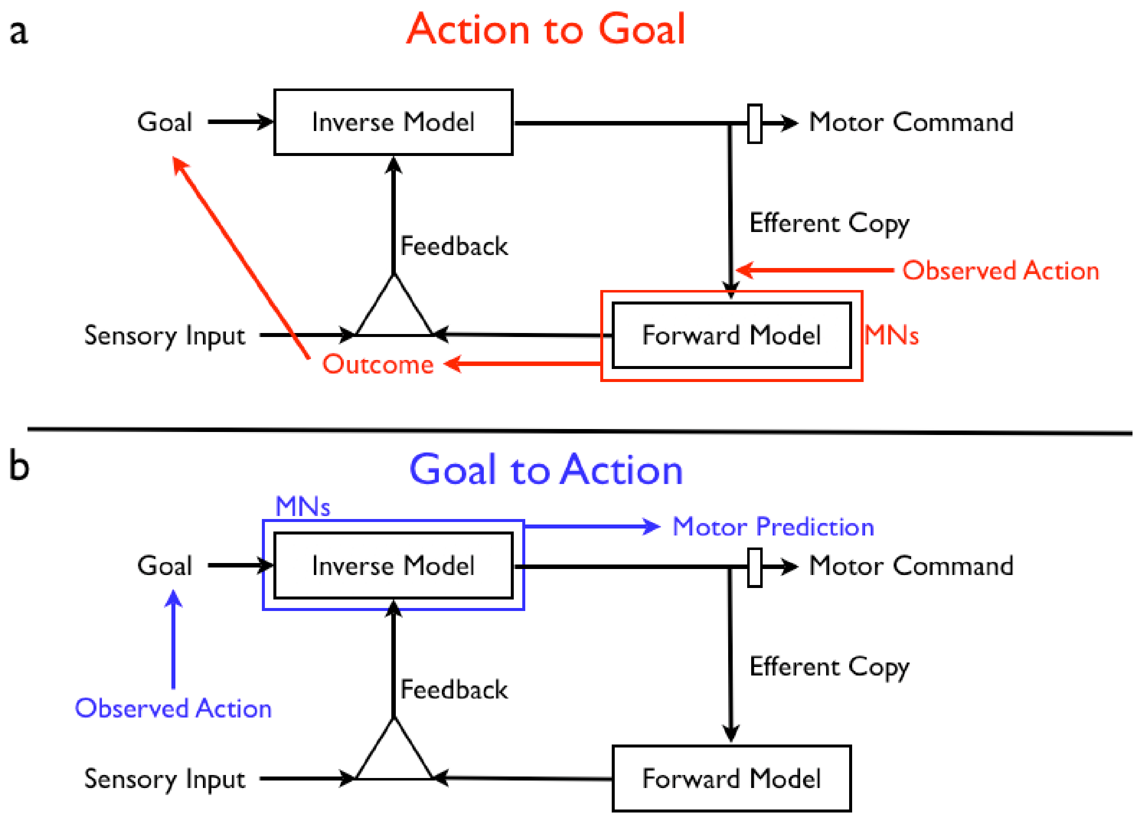

Figure 1. **Mirror neurons in a simple motor control loop.** A motor act is initiated by the desired end state ("Goal"), which is translated by a motor controller (the "Inverse Model") into a Motor Command. A copy of the motor command can be used by the corresponding predictor ("Forward Model") to produce the expected sensory effect of the motor command. This prediction can be compared to the incoming Sensory Input, and any resulting error term could be fed back to the Inverse Model. Note that the loop can also be activated off-line, without executing the motor command by the effectors. **a)** If mirror neurons perform action-to-goal computations, they may rely on the forward models of the control loop, which turns the mirrored motor command into an outcome prediction. The outcome of an action normally matches the goal that initiated it. **b)** If mirror neurons perform goal-to-action computations, they represent the inverse models of the control loop. In this case, the observed action is interpreted outside the motor system, and its hypothesized goal is fed into the inverse model, which turns it into an action prediction.