

**Mirror neurons and their potential role in action understanding, imitation and evolution of language:  
An overview of the past two decades of research.**  
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## Abstract

Mirror neurons are a class of neurons that respond both when a subject executes a motor action and when the subject observes (either by means of visual or auditory stimuli) the same action being performed. This paper aims to provide an overview of the past two decades of research on the subject, focusing on the potential role of mirror neurons in action understanding and imitation. In addition, the potential role of mirror neurons in the evolution of language, autism, empathy and stroke rehabilitation will be briefly reviewed, however, a detailed discussion of these subjects is beyond the scope of this paper. It concludes that it is likely that the mirror neuron system underpins action understanding, as part of a greater cognitive network. It is unclear whether mirror neurons play a role in motor imitation, and if they do, it is equally unclear what the specifics of that role would be. It is becoming increasingly more likely that mirror neurons have played a role in the evolution of language, though the topic is still hotly debated. The research on the role of the mirror neuron system in other fields, such as autism, empathy and stroke rehabilitation is still at too early a stage to draw any conclusions, though early results are discouraging for their role in autism, and encouraging for their potential in stroke rehabilitation.

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## Introduction

Mirror neurons are a class of neurons that respond both when a subject executes a motor action and when the subject observes (either by means of visual or auditory stimuli) the same action being performed (1). Since they were first discovered in the macaque monkey in the 1990s (2, 3) they have by some been hailed as one of the single greatest discovery in systems neuroscience of the past few decades (4, 5). As often happens when scientist come across a new and unexpected finding, a flood of potential functions for these cells were proposed, ranging from action understanding (3, 6), motor imitation (1, 7-12), empathy (13, 14), stroke rehabilitation (15-17), evolution of language (3, 18) and cause of autism (19, 20), to the seed of human civilization (21) and our preference for romantic movies (22). But what do we actually *know* about mirror neurons?

This paper will attempt to provide an overview of the past two decades of research, focusing on the potential role of mirror neurons in action understanding and imitation. We will begin by describing the first experiments in which mirror neurons were first described and categorized, followed by a summation of the key findings related to the behavior and anatomy of the mirror neuron system in monkeys. This is followed by an overview of the mirror neuron system in humans, with emphasis on the difference between the human and the monkey mirror neuron system. In the discussion portion of this paper, the following questions will be debated: Do mirror neurons in fact exist or have the original findings been invalidated? What role, if any, do mirror neurons play in action understanding? What role, if any, do mirror neurons play in imitation? In addition, the potential role of mirror neurons in the evolution of language, autism, empathy and stroke rehabilitation will be briefly reviewed, however, a detailed discussion of these subjects is beyond the scope of this paper. Still, references to excellent articles on the subject will be provided for the interested reader to study at his or her own leisure.

## Method

This paper is a mandatory student assignment, required to progress to the last year medical studies at the University of Oslo. The subject was chosen by the author, due to the author's own curiosity of the subject. There are no conflicts of interest.

While working on this paper, the author has been privileged to receive the helpful guidance of Professor Arild Njå, Ph.D., Departement of Physiology, Institute of Basic Medical Sciences, University of Oslo, who has provided ample advice and references, along with constructive criticism and counsel.

The references and material for this paper were gathered by means of an online PubMed search, using the following search terms: "mirror neuron", "mirror neurons" and "mirror neuron system". The author then proceeded to find reviews already written on the subject, and used these reviews to find the original articles upon which the reviews were based. In addition, a search for individual articles published from 2010 and up to the present day was performed, as these articles might have been overlooked by even the more recent reviews (as indeed some were).

Special care and attention was aimed at finding several different reviews and articles on each subject that were both outwardly positive and outwardly negative to the given findings. This was done in an attempt at assuring that the basis of the authors own conclusions were not biased.

The review articles chosen were assessed in the following way: Some were discarded by title alone. Others were excluded after examining their abstracts. The ones found to be pertinent to this paper, were further assessed: The stated purpose of the review was evaluated, along with the criteria of inclusion/exclusion of individual articles, the method for finding

said articles, and the potential bias of the authors were all reviewed. The latter was often present due the majority of the papers published on the subject being written either by the researchers that originally discovered these neurons, or by scientists defending their own established theories that are threatened by this new discovery. This bias was taken into account when evaluating their contents.

The individual articles were assessed in the following way: Some were discarded by title alone. Others after examining their abstracts. The ones found to be pertinent to this paper, were further assessed: The stated purpose of the article was evaluated, the method used for examining the stated purpose were reviewed. If experimental studies: whether the conclusions were reasonable based on their findings, along with the potential bias of the authors were evaluated.

## Results

**The first discovery.** Mirror neurons were first discovered entirely by chance while studying the motor neurons of the inferior premotor cortex of a *Macaca nemestrina* monkey, specifically those responsible for arm movement, located near the arcuate sulcus, largely coextensive with the histochemical area F5 (23). The original aim of the experiments was to study the activity the motor neurons in a behavioral setting, where one could distinguish between stimulus associated responses from the activity related movements. The monkey was trained to retrieve objects of different shapes and sizes from a box, with a variable delay after a stimulus presentation. However, after the initial recording, it was incidentally observed that some of the experimenter's actions would activate a large portion of the F5 neurons, despite there being no apparent movement by the monkey (2).

Following this discovery, new experiments were conducted in an attempt to describe the properties of these neurons. For this purpose, the electrical activity from single neurons was recorded from sector F5 of two macaque monkeys, while simultaneously recording the actions of the monkeys and the experimenter. In the first monkey, activity from both the left and right hemisphere was recorded, while recordings were only made from the left hemisphere of the other monkey. A total of 532 neurons were recorded, of which 92 displayed characteristics of mirror neurons (3).

As we shall see, the majority of the mirror neurons respond only to the observation of a single action, and can therefore, for simplicity's sake, be grouped and named by the action that activates them, for example 'grasping neuron'. Though there were some neurons that responded to more than one action, they will not here be described in detail, because other than their lesser specificity, no additional distinguishing characteristics could be determined (3).

*Grasping neurons* respond to the sight of a hand approaching and grasping an object. The trial began with the presentation of the stimulus to the monkey (a raisin on a tray). At this stage, no discharge was seen, however once the experimenter reached for the object (as soon as hand shaping began) the neuron began to fire. Some grasping neurons stop firing almost as soon as the hand grabbed the object, while others continued for a short while afterwards. There was no firing when the tray was moved towards the monkey, but it began to discharge once more when the monkey itself grasped the raisin (3). When the experimenter attempted to grasp the raisin with a tool (a set of pliers), a similar, albeit weaker, response was observed (3). Furthermore, a subset of grasping mirror neurons were discovered ( $n = 18$ ), that only responded to a particular manner of grasping. For example, a neuron may respond to a precision grip, but show no response when using a whole-hand prehension. Mimicking the grip or action in the absence of the object also elicited no response (3).

*Placing neurons* discharge when moving a stimulus towards a plane or support. They start to fire when an experimenter, for example, places a piece of food on an empty tray, and they stop firing when the hand starts moving away from the food. The grasping of the same food from the same tray by the experimenter elicited a much weaker response (3).

*Manipulating neurons* respond when an experimenter touch or move an object with his fingers in order to take possession of it, for example taking a raisin out of a well. They started to discharge just before the finger touched the food and stopped once the food was retrieved. The mimicking of the movement without an object present elicited a much weaker response, while the retrieval of the food with a tool elicited no response at all (3).

*Hands interaction neurons* responded best to the movement of one hand towards another hand, when one of the hands was holding an object. Firing begins at the start of the movement and ends once the hand touched the other and began to move back. The same movement without any object (e.g. food) elicited a weaker response, and a weaker still reaction was observed with the use of tools, for example a disc with a long handle moved towards a similar disc in the other hand. No response was seen when simply grasping an object (3).

*Holding neurons* discharged when the monkey observed an object being held in the hand of the experimenter. The firing ceased as soon as the experimenter's hand moved away from the object. With the exception of two neurons, all holding neurons also elicited a response to the observation of other actions (3).

*Mirror-like neurons* (n = 25) displayed the same behavior as above for the observation of hand actions, but had no motor functions (3).

32 neurons were also tested for hand preference, with the action being performed in front of the monkey and on each of its sides. 12 neurons (37.5 %) displayed a marked preference; 9 to the ipsilateral side, 3 to the contralateral side. The preferred hand for the monkey's active movements was often the opposite of the visual preference, as one might expect since in a face to face stance, the hand of the acting individual is the opposite of the observer's hand (3). Furthermore, of 47 mirror neurons tested, 30 displayed a marked preference for the direction an action was performed, e.g. from left to right. 83.3 % of these preferred the direction towards the side of the hemisphere in which the neuron was located (3).

Most mirror neurons had an obvious relationship between the effective observed action and the effective motor action. Based on the specificity of this link, the neurons can be subdivided into three groups: (i) strictly congruent (n = 29; 31.5%), which responded only when both the general action and the way in which the action was performed corresponded, for example firing only when observing or performing a precision grip, but no other form of grasping or hand action; (ii) broadly congruent (n = 56; 60.9%), for which there was a clear link between the observed action and the motor action, but they were not identical. Some (n = 7) were highly specific in terms of motor activity, e.g. reacting only to precision grip, but would respond to the observation of many types of grip. Others (n = 46) would fire during one type of motor action, e.g. grasping, but respond to the observation of several types of actions, e.g. grasping and manipulation. The last group of broadly congruent mirror neurons (n = 3) seemed to respond the goal of the action, rather than the means by which it was achieved, e.g. firing during grasping with the hand, but responding to the observation of grasping either with the hand or the mouth. (iii) Finally, for some neurons (n = 7; 7.6 %) no clear link between the effective motor action and the effective observed action could be determined (3).

To exclude the possibility that no hand or mouth movements were made by the monkey during the observation phase that were not seen by the experimenter, and that might explain these findings, multiple sessions of electromyography (EMG) recordings from several hand and mouth muscles were performed expressly for this purpose. There was no recorded activity during the observation phase (3). As an additional precaution, a total of 49 neurons

from the hand field of the F1 area (primary motor cortex) were recorded, the thinking being that if the observation of the experimenter's actions would trigger some comparable movement in the monkey's F5 region, it should also activate the neurons in the F1 region that control them. None of the neurons showed any activity during the observation phase (3).

Furthermore, because the monkey would usually be watching its own movements, the behavior the recorded neurons displayed during the monkey's actions could be due to the neuron's visual properties alone rather than its motor properties, or a combination of the two. To control for this, a set of mirror neurons ( $n = 14$ ) were tested in both light and dark conditions. All neurons fired the same way in both situations, which was also consistent with the more informal testing of other mirror neurons (3).

**Goal-related response.** Following the publication of the above mentioned findings, a series of experiments have been conducted that further elaborate, expand and differentiate our understanding of the mirror neurons.

Since it was known that ventral part of the F5 area contains neurons that respond to somatosensory stimulation of the region surrounding the mouth (24), it was not unreasonable to propose the existence of a mouth mirror neuron system in the area. To investigate this, similar experiments to the ones mentioned above were made for mouth movements. Of the 470 neurons that displayed motor responses related to mouth movements, 180 neurons (~49%) also displayed visual responses, with 72% of these ( $n = 130$ ) firing during the observation of mouth movements, thus confirming their assumptions (25). 85% of the investigated mouth mirror neurons discharged when observing goal-directed ingestive actions, with grasping, breaking and sucking being the most effective triggers. Using the same classification system as above, 37% of the mouth mirror neurons were classified as strictly congruent and 58% as broadly congruent (25); these numbers being remarkably similar to those for hand mirror neurons in the dorsal F5 area (3).

Interestingly, the researchers also examined the visual response to communicative mouth movements, such as lip-smacking and lip- and tongue protrusion. 15% ( $n = 12$ ) responded strongly to the observation of these movements, with only a weak response to the observation of ingestive movements, suggesting that ingesting and communication in the monkey share the same neural basis (25).

Another experiment was conducted on the basis of the everyday observation that primates can understand the goal of an action even if this action is partially hidden from view, e.g. if a person reaches towards a bookshelf most people will be able to understand that the person is about to pick up a book, even if said book cannot be seen. In other words, if mirror neurons are indeed goal-oriented, they should respond to the observation of an action, even if some the action is hidden, assuming enough information is available to be able to determine what the goal of the action is. The experiment involved recording the response of 220 mirror neurons in the F5 area under four conditions. (i) in full vision the monkey would observe the experimenter grasp an object or (ii) mimic the same action in the absence of the object. In the hidden condition, the monkey would first be shown if an object was present, and then the final part of the action would be concealed by an opaque screen - the experimenter would then (iii) grasp the object, or (iv) mimic the action in the absence of the object. Fifty-one% ( $n = 19$ ) of the 37 tested mirror neurons discharged also during the hidden condition with an object present, but showed no response when the object was absent, thus confirming their initial theory (26).

The same line of thinking led to another experiment to see if sound could trigger the same kind of response as visual stimuli. 497 neurons of the F5 region were studied under 4 separate conditions: (i) motor, in which the monkey executed the action; (ii) visual-only, in which the monkey observed an experimenter perform the action; (iii) auditory-only, in which

the monkey listened to sounds associated with the action; and finally (iv) audio-visual, in which the monkey observed the action being performed while listening to the associated sound (27). 13% (n = 63) of the studied neurons responded to auditory stimuli, with the most effective sound in triggering a response being peanut breaking and ripping of paper (76%; n = 48). Other sounds to which there also was a response were: crumbling of plastic (n = 5), metal hitting metal (n = 3), shaking paper (n = 3), manipulating dry food (n = 2) and dropping a stick (n = 2) (27).

Another experiment was conducted to test for the specificity of the auditory mirror neurons. Of a total sample of 286 neurons in area F5, 61 exhibited auditory responses (21% of total sample, 47% of mirror neurons in sample), though only 33 of them could be kept long enough to test them in all experimental conditions. Of these, 88% (n = 29) discharged significantly stronger when the monkey listened to one sound, when compared to another. And of these 29 neurons, 16 neurons (~55%) displayed almost the same behavior in the visual-only and in the auditory-only conditions the given action, 10 neurons (~34%) preferred the audio-visual condition, with the remaining 3 neurons (~10%) showing a stronger response in the auditory-only condition (28).

**Use of tools.** An important question to answer about the mirror neuron system is to what degree, if any, it displays plasticity in the adult brain. Peculiarly, the author of this paper has not been able to find any article that examines this directly. There are however, some indirect findings. As you may recall, in the original experiments published in 1996 the monkeys had not been exposed to tools, and the use of tools in goal-directed actions triggered either no response or a very weak response in the studied mirror neurons (3). In another experiment, two monkeys had for several months both observed the use of tools in goal-directed actions and performed the same action with the same tools. After this period, 209 neurons in the F5 region were studied, 143 of which were classified as mirror neurons, and their activity was recorded during the execution and observation of goal-directed action both with the use of tools and biological effectors (such as hand or mouth). 42 neurons (29%) fired during the observation motor acts performed with the use of a tool. 33 of these were examined more closely, and all of them discharged more during the observation of a motor act performed by a tool, than by a biological effector (29). If one considers this result with that of the earlier experiments, the findings suggest that the amount of tool-responding mirror neurons increased with time due to exposure, indicating that the mirror neuron system indeed does have some degree of plasticity.

The fact that the use of tool, when properly conditioned, could trigger responses from the mirror neuron system, allowed Rochat et al. to conduct another interesting experiment. First, they trained two monkeys to grasp food with reverse pliers (30). Then they recorded the responses of 282 hand-grasping neurons, 92 of which were classified as mirror neurons, and 27 of these were recorded in 4 separate scenarios: grasping of food and observation of the same with either the hand or the reverse pliers. 20 of the recordings were used for analysis, of which 18 (90%) discharged during all four conditions. No significant difference in intensity was observed when the execution of the motor act with a hand compared with the use of pliers, though they did respond with greater intensity to the observation of the action done by hand when compared to the use of pliers (31). These results offer a perhaps even clearer indication that at least a subset of mirror neurons encode the goal of the action, rather than the action itself.

As a continuation of this experiment, 16 of the above mentioned 20 neurons, were further tested during the observation of spearing of food with a stick by the experimenter, a tool which the monkey had neither seen nor used before. 12 of these neurons responded even in this condition, and though the response was significantly weaker than when observing the

grasping by hand or by use of pliers, the response was still significantly greater than baseline. This finding might suggest that the information encoded by the mirror neurons is not of a binary nature, but that the intensity of the discharge might allow for some differentiation of the observed motor act. The observation of motor acts already in the subject's repertoire should then elicit a strong response, while the observation of actions that the subject does not perform itself but shares enough similarities to one that the subject does perform, should elicit a weaker response (31).

**Inhibitory mechanism.** The discovery of mirror neurons in the ventral premotor cortex begs the question, why do the monkeys not move when observing a motor act? After all, it is the same neuron firing both during the observation and the execution of a given action. A possible explanation is that the F6 area (rostral part of mesial area 6) works as a sort of switching mechanism, at least for arm movements, controlling the activity of the ventral premotor areas during action observation. Indeed, activity in area F6 is required for a potential motor action to be acted upon, making sure that a movement is only performed when external contingencies and motivational factors are appropriate (32).

Another possible explanation, that is not mutually exclusive with the above, was discovered when Kraskov et al. wanted to examine the possible existence of mirror neurons in the pyramidal tract, since it was known that the F5 area also contributed to the cortico-spinal tract (33). The visual responses of 48 neurons in the pyramidal tract were recorded in two monkeys, and as much as 52% of these ( $n = 25$ ) were classified as mirror neurons. But even more surprising was that approximately half of these ( $n = 14$ ) displayed opposite reactions to the observation and to the execution of a motor act, i.e. they increased their firing rate during action execution, but decreased their firing rate during action observation. Moreover, the visual response of these "suppression PT mirror neurons" peaked earlier and was more protracted, when compared to the regular "facilitation PT mirror neurons" that responded the same way to both the observation and execution of an action. Based on these findings, the authors suggested that these neurons may be part of the system that inhibits self-movement during action observation (34).

**Distance and operational space.** Another fascinating discovery was also made by coincidence, when in preparation for an experiment designed to perform another quantitative analysis of mirror neuron responses the grasping of objects, in which objects were placed on a tablet that could detect and log the time at which the objects were grasped and lifted from it. By chance, it was discovered that while the neurons fired as one might expect when the tablet was placed at some distance from the monkey, when the tablet was placed closer, the firing ceased, suggesting the possibility that some mirror neurons were distance-specific. Tests were conducted to examine this aspect, and of the 105 neurons tested, 52% ( $n = 55$ ) changed their behavior when the distance to the manipulated object was changed. Specifically, 49% of these ( $n = 27$ ) discharged more strongly when the object was within the monkey's peri-personal space, with the remaining 51% ( $n = 28$ ) discharged more strongly when the object was outside of the monkey's peri-personal space (35).

If these mirror neurons were indeed distance-specific, one can imagine two possible ways in which this is encoded: (i) metric encoding, in which the distance is fixed, depending only on the distance of the object from the monkey or (ii) operational encoding, in which the response depends on the current workspace of the monkey. This was investigated by introducing a frontal panel to the experiment, which would prevent the monkey from reaching objects close to it. Interestingly, of the 21 neurons tested under such conditions, a full 43% ( $n = 9$ ) changed their behavior and started either to respond to the observation of action performed in the monkey's peri-personal space when before they responded only to the



observation of actions performed in the extra-personal space, or they stopped responding altogether if they used to the observation in the peri-personal space. This suggests that at least some of the mirror neurons use operational encoding, and that the behavior of mirror neurons is not exclusively modulated by the goal of the action (35).

Furthermore, if the monkey's operational space influences the response of the mirror neurons, it is conceivable that they also contribute to the selection process of appropriate behavior to a given observed action, and if so, they might also be modulated by the perceived potential reward of an action. To test for this, an experiment was conducted in which the same motor act, i.e. a power grip, was performed in front of a monkey on two separate objects: a large grey cylinder and a smaller red cylinder. After gripping the grey cylinder nothing would happen, but after gripping the red cylinder the monkey would be rewarded with some food. Out of a total of 87 neurons tested, 40 (46%) fired more strongly when the hand gripped the red cylinder, 36 neurons (41%) displayed no preference, while only 11 neurons (13%) preferred the grey cylinder. This was interpreted to indicate that in addition to encoding the goal of a motor act, the mirror neurons might also encode the subjective value of a given motor act to the observer (36).

**Other brain regions with mirror neuron behavior.** At the time mirror neurons were first discovered in the mid-90s, the existence of other neurons with similar responses to action observation had already been found in the upper bank of the superior temporal sulcus (STS), though they had no known motor properties (37, 38). This led some to theorize that the F5 area and the STS were part a cortical network that involved action perception, and indeed, though not directly connected, anatomical studies had shown that the two regions were bi-directionally linked via the rostral part of the inferior parietal lobule (39, 40). Before long, the existence of mirror neurons in the inferior parietal lobule had been determined (41), and several experiments were conducted to characterize these and compare them to those in area F5.

One of these, compared the motor responses of 139 neurons in the F5 area to the motor responses of 120 neurons in the PFG area, during the execution of two motor actions, each consisting of two motor acts: grasping a piece of food and then bringing it to the mouth, or grasping a piece of food and placing it in a container. As expected, the majority of the PFG motor neurons were action goal related: 55% ( $n = 66$ ), a number highly consistent with previous studies (42, 43). 79% ( $n = 52$ ) fired more strongly during grasping when it was followed by bringing the food to the mouth, while 21% ( $n = 14$ ) fired more strongly during the grasping of food when it was followed by placing it in a container. The action goal related motor neurons of the F5 area were similarly distributed, with 60% ( $n = 32$ ) firing more strongly during the grasping of food when the act was followed by bringing it to the mouth, and 40% ( $n = 21$ ) fired more strongly the grasping was followed by placing the food in a container. However, the PFG area had a significantly greater proportion of action goal related neurons when compared to area F5, 55% vs. 38% respectively (43).

Next, they compared the visual responses in the two areas, and again, as expected, they found that the majority were action goal oriented neurons, but they found no significant difference in the proportion of these neurons in the two areas: 64% in area PFG vs. 66% in area F5 respectively. This might suggest that there was no significant difference in the visual encoding of the motor acts in the two areas, but that the inferior parietal lobe might have an important role in working with area F5 to encode complex chains of motor acts (43).

Indeed, in real life, most motor acts are performed in a complex chain of events, with the intention of the act often only becoming apparent towards the end of the motor chain's conclusion. To investigate how mirror neurons behave under such conditions, an experiment was devised in which the final goal of a monkey's action, consisting of three motor acts in

total, would only become apparent as the action unfolded: The first act involved grasping and lifting the lid of a box. The second act involved grasping the contents of the box, using the same grip. The final act however, would depend on the contents of the box: if it was food, the monkey would eat it; if it was a small metallic object, the monkey would place it (44). They found that the studied mirror neurons could be broadly classified into two groups: No-preference neurons, that displayed no difference in their response to either eating or placing conditions, and Action-Goal-Related neurons, that did display a distinct preference. The latter group was further subdivided into two: Early-preference neurons, that fired differently both during the lid and the target grasping, and Late-preference neurons, that only fired differently during the target grasping. A possible interpretation of this finding, is that the different types of neurons encode the action goals at different levels of abstraction, i.e. that the No-Preference neurons encode the actions independent of the action goals, the Late-Preference neurons encode the goal of the action when all of the information of the final goal is available, while Early-Preference neurons encode the intention of the monkey at the start of the motor action, which is then modified as the action proceeds based on the sensory cues available (44).

Interestingly, the relative distribution of these neurons differed in area F5 when compared to the PFG area. Of the Action-Goal-Related neurons in the PFG area, 73% ( $n = 47$ ) were Late-Preference neurons and 27% ( $n = 17$ ) were Early-Preference neurons. In the F5 area however, only 7% were Early-Preference neurons, with the remaining 93% ( $n = 26$ ) being Late-Preference neurons. In line with the thinking in the previous paragraph, this suggests that area F5 is more concerned with encoding the immediate goal of the action, while the PFG area is more involved in the relative long term intentions of the action (44).

Furthermore, if the mirror neurons encode only high-level aspects of an observed action, i.e. the goal and intention of the action, then it is reasonable to assume that the visual response of mirror neurons would abstract from the point of view from which an action is perceived. To explore this further, Caggiano et al. devised an experiment in which a monkey was first shown a goal-directed action in real life and the same action on film, while recording the response of mirror neurons in the F5 area. Of the 123 investigated neurons that responded to the visual stimuli, 53 neurons (43%) displayed a stronger response the naturalistic actions, 17 neurons (14%) preferred the filmed actions, while the remaining 53 neurons (55%) showed no preference at all (45). In the second phase of this experiment, the monkey was shown footage of the same goal-directed motor act, but viewed from three different angles: first-person perspective, third-person frontal view and third-person side view. Surprisingly, they found that a clear majority of the neurons (74%,  $n = 149$ ) displayed a view-dependant behavior, with the first person perspective being the most common preference (45). Caggiano et al. suggested that perhaps the view-independent neurons encode the goal of the action, ignoring the details of the motor action, while the view-dependent either play an earlier part in the process of abstracting the motor action's intention, or, alternatively, that they contribute to the top-down modulation of the visual patterns associated with a motor act by the F5, PFG/AIP and STS regions, i.e. that the view-dependant neurons might modulate the visual representations in the STS, thereby reinforcing the processing of visual patterns associated with different points of view (45).

**Mirror-like activity.** There are other experiments that have results documenting neuronal activity highly reminiscent of mirror neurons, though they were not classified as such in the published articles. An example of this can be found in the series of experiments performed by Cisek and Kalaska to investigate how a monkey's brain maps multiple reaching directions. For the experiments, they trained a monkey to perform a "center-out reaching task" in a horizontal plane, in which the eight possible targets were distributed along a circle, marked by colored circles. First two of these circles lit up and then disappeared (spatial cue).

This would be followed by a centrally located circle lighting up, informing the monkey which of the two targets it is supposed to reach for (color cue). Then the central circle would disappear, all eight circles light up, a go-signal issued, and the monkey would perform the task. However, during the experiment, the monkey would not be able to see its own arm, and all visual feedback was provided via a screen with the target represented on it, along with a motion cursor representing the position of the arm (46). During the spatial cue phase, they recorded neuronal signals from the dorsal premotor cortex, suggesting that the representation for the two possible target directions were both active. During the color cue phase, the selected direction was enhanced, while simultaneously the deselected direction was suppressed. This might indicate that multiple potential movement options are represented at the same time in the same system (47, 48).

An even more fascinating result was achieved when the monkey was simply asked to observe the screen while the experimenter performed the same tasks as described above. A full 84% of the studied neurons that were active during the execution of the tasks, were also active during the observation of the tasks alone, even displaying the same directional tuning behavior (49).

A similar experiment to the one described in the two previous paragraphs was also performed with the monkey observing an experimenter perform the task directly, without the need for the abstract representation of the screen. Roughly 46% of the neurons in the M1 region that were active during the execution of the task, were also active during the observation alone (50). However, following this experiment, the researchers also examined if there was a difference in the directional tuning of the neurons during the action execution phase and the action observation phase. They found that the majority (68%) of the neurons displaying directional tuning behavior in both conditions, had different directional preference in the two scenarios, i.e. they preferred one direction during action observation, and another during action execution. The remaining 32% had the preference in both scenarios (50). Interestingly, this latter number is remarkably close to the proportion of strictly congruent mirror neurons found in area F5: 31,5% (3).

To investigate this further, the researchers trained a classifier with the population results collected during either action execution or action observation in cases where neurons displayed directional tuning behavior, and then tested the predictive capabilities of the classifier on individual trials. As one would expect, high recognition was seen when the direction of a given motor action was predicted using a classifier trained on recording from trials of task execution, and when the direction of an observed movement was predicted using a classifier trained on recordings from trials of task observation. However, the results were close to chance level when trying to predict the movement direction in trials of task execution using a classifier trained on the activity from observation trials, or to predict the movement direction in trials of task observation using a classifier trained on the activity from execution trials. This finding might suggest that the neurons in M1 that respond both during action execution and during observation, encode different features for each of the two scenarios, and if so, they might serve different functions in each scenario (50).

**Non-visuo-auditory stimuli.** In addition to motor responses, reports of other mirroring phenomena are beginning to emerge. One example of this was found when studying the visuotactile responses of neurons in the ventral intraparietal sulcus and area 7B. These neurons were known for responding both when the monkey itself was touched and when an object was moved close towards the monkey's body (51). Based on this, an experiment was conducted in which a monkey observed an object be moved towards and away from an experimenter's body, who would otherwise be sitting still. Of the 541 neurons studied, 48 responded in this scenario as well, and could be classified into three groups based on their

behavior: (i) mirror-image matching neurons, for which the visual receptive field of the monkey was contralateral to that of the experimenter's; (ii) anatomical-image matching neurons, for which the visual receptive field of the monkey was ipsilateral to that of the experimenter's; and (iii) central matching neurons, for which the visual receptive field was close to the midline in both subjects (52).

**Other animals.** Before we turn our attention to humans, it also bears mention that evidence of mirror neurons in other animals besides primates have been reported. One of the interesting findings have been made in birds, where one has seen activation of the same neurons during both the performance and listening of birdsong, and there are even indication that these neurons play an important role in the process of learning vocal production (53, 54). In addition, there have been speculations that, among others, dolphins, elephants and dogs possess a mirror neuron system (55).

**EEG and TMS studies in humans.** Following the first reports of mirror neurons in macaque monkeys, the search for evidence of the existence of an analogous system in humans began. For obvious ethical and practical reasons, it is very difficult to do studies with human subjects in which single neurons are recorded, and as such, there is very little in direct evidence of the existence of mirror neurons in humans. There are however plenty of indirect studies, mostly in the form of neurophysiological and brain-imaging experiments (56). These are for the most part made under the widely held assumption that human homologue of the macaque monkey area F5 are the ventral premotor cortex and the pars opercularis of the posterior inferior frontal gyrus (Brodmann area 44), and that the rostral inferior parietal lobule is the human analogue to the PF/PFG area of the macaque monkey (1, 57, 58). In other words, one would expect that the inferior frontal gyrus and the inferior parietal lobule should be reliably activated when the human subjects are engaged in tasks design to elicit a response in the mirror neuron system. However, if the mirror neuron system in humans is more widespread in the human brain, as some have suggested (59, 60), then regions outside the ones mentioned above would also be activated, depending on the task being examined. It ought to be stressed however, that in contrast to the monkey, when one refers to the "human mirror system", one is referring to brain *regions* that are active during both action observation and executions.

That part of the human motor cortex becomes active during the observation of an action performed by another individual in the absence of any evident motor activity by the studied subject, has been known since the mid-1950s, on the basis of observed desynchronization on electroencephalography (EEG) recordings of the so-called mu rhythm that occurs both during action observation and execution of the same action (61, 62). This finding was confirmed both by new EEG recordings (20, 63-65) and by the use of the magnetoencephalography (MEG) technique, which also showed that the desynchronization included rhythms originating from the cortex within the central sulcus (66-68).

Several transcranial magnetic stimulation (TMS) studies have also been performed specifically to investigate the human mirror neuron system; one such study involved recording motor evoked potentials (MEPs) from the right hand and arm muscles (from stimulation of the left motor cortex) in subjects observing both transitive motor actions (grasping an object) and intransitive motor movements. They found that the observation of both transitive and intransitive motor movements elicited an increase of recorded MEPs, which was selective to only those muscles which would participate in producing the observed movements (69). In other words, unlike the monkey mirror neuron system, it appears as though the human mirror neuron system also codes for intransitive movements, a finding which has been reproduced in other similar studies (70, 71).

The temporal aspects of cortical facilitation during action observation was examined by Gangitano et al. by recording MEPs from hand muscles elicited by TMS in human volunteers, while they observed various grasping movements made by another human subject. These MEPs were recorded at varying intervals during the movement, and the results showed that the cortical excitability of the observers closely followed the phases of the observed grasping movements (72).

There are also studies suggesting the existence of a human inhibitory mechanism in the spinal cord, supposedly similar to the one described above for monkeys (34). The experiment involved the measurement of the H-reflex in the flexor and extensor muscles of the arm of human volunteers, during the observation of the opening and closing of a hand by another human. The size of the H-reflex from the flexor muscles increased during the observation of the hand opening, and decreased during the observation of hand closing. The opposite was true for the extensor muscles. This suggests that there exists an inhibitory system in the spinal cord that prevents the execution of the observed action (73).

**fMRI studies in humans.** A number of functional magnetic resonance imaging (fMRI) studies have also been conducted. One such study involved the presentation of video clips showing various motor actions performed with the mouth, hand, arm, foot and leg to human volunteers. Static images of face, hand and foot were used as controls. The observation of object-related mouth movements activated bilaterally the inferior precentral gyrus and the pars opercularis of the inferior frontal gyrus. In addition, two foci in the parietal lobe were also activated, one located rostral part (most likely area PF) and the other in the posterior part of the inferior parietal lobule. Object-related hand/arm actions activated the pars opercularis of IFG and a foci in the precentral gyrus, along with two foci in the parietal lobe. Finally, object-related foot/leg actions activated a dorsal area of the precentral gyrus and also in the parietal lobe (in part overlapping the area activated by mouth and hand/arm actions, but also extending more further dorsally). Together, these findings suggest that the mirror regions in humans are somatotopically organised (74).

Interestingly, in all of the above mentioned cases, intransitive movements activated the same regions as the transitive actions, with one exception: the parietal lobe remained seemingly inactive (74), and this finding has been verified in a number of similar studies (9, 12, 75). Since it is known that the premotor areas receive visual information from the inferior parietal lobule, it is difficult to understand why the inferior parietal lobe was not active during intransitive movements. Some have suggested that it is active in both cases, but that it is stronger in the presence of an object, and that in the absence of an object the activity is not strong enough to be statistically significant (1).

Another fMRI study investigated how the mirror neuron system responds to motor actions performed by species other than humans. Video clips of silent mouth actions in the form of biting and various oral communicative action (i.e. lip smacking, barking, speech reading) performed by monkeys, dogs and humans were shown to human volunteers. The observation of biting activated the same brain regions in the subjects, regardless of which species performed the action: pars opercularis of the IFG, the adjacent precentral gyrus, and two foci in the inferior parietal lobule, bilaterally. The only difference observed was a stronger activation on the right hemisphere of the above mentioned regions when the action was performed by a human. As for the communicative gestures: lip smacking by the monkey activated a small foci in the pars opercularis of the IFG bilaterally, speech reading by the human activated the left pars opercularis of the IFG, and finally, barking by the dog did not produce any activation in the frontal lobe (76). These findings have interpreted to suggest that the motor actions that are already part of the motor repertoire of the observer are mapped on

the person's motor system, while those not part of the observer's motor repertoire are mapped on a visual basis (1).

Another fascinating fMRI experiment was conducted by Johnson-Frey et al. to see if the mirror neuron system requires dynamic hand movements or if the goal of the action alone is sufficient. To test for this, human subjects were shown static images of objects being either grasped (either in a functional or non-functional way) or simply being touched. Both usable objects (bottle) and an ambiguous object was used. In all 17 subjects, the presentation of a static image displaying a goal-related action was sufficient to selectively activate the mirror neuron region in the frontal cortex (77).

**Imitation.** Other fMRI studies have been done with an emphasis on imitation. One such experiment tasked human volunteers to observe either the lifting of a finger, a cross on a motionless finger or a cross on an empty background. In the next phase, they were asked to lift their own finger as soon as they saw the aforementioned stimuli. Interestingly, they found that some brain regions responded more strongly when the subjects had to lift their finger in response to observing another finger being lifted (i.e. during imitation) than to any of the other stimuli. These areas were: the left pars opercularis of the IFG, the right anterior parietal region, the right parietal operculum and the right STS region (10, 12). A similar experiment confirmed these findings, and also found that Broca's area was particularly active when there was a goal to the action being imitated (9). The activity of Broca's area during imitation was further confirmed by use of MEG (11).

As a follow-up, another MEG study was performed, this time looking at mouth movements. Human subjects were tasked to observe pictures of both verbal and non-verbal lip grimaces, to imitate them spontaneously or to imitate them directly after having seen them. During observation alone, the cortex activated in the following order: from the occipital cortex to the superior temporal region, the inferior parietal lobule, IFG (Broca's area), and lastly the primary motor cortex. When asked to imitate directly after observation, the same sequence of activation was seen, however, when they merely performed the same movements spontaneously, only Broca's area and the motor cortex became active (8).

An even more fascinating study was done by means of repetitive TMS (which temporarily interrupts the functioning of the targeted area). The human subjects were tasked to either imitate the pressing of a button with a finger, or to simply execute the action after the presentation of a spatial cue. During the execution of these tasks, they received repetitive TMS (rTMS) over the left and right pars opercularis of the inferior frontal gyrus (Brodmann area 44) and over the occipital cortex. Imitation was severely impaired when pars opercularis was stimulated, but not during the stimulation of the occipital lobe. The execution of the same task without imitation was seemingly unaffected by the rTMS (7).

Another fMRI experiment studied cortical excitation during the imitation of guitar chords played by a musician, by naive human participants during 4 stages: action observation, pause, guitar chord execution and finally rest. Additionally, some were tasked with merely observing the action with no subsequent motor action of their own, some would follow their observation by a non-related motor action (e.g. scratching the guitar neck), and lastly, some were tasked to freely perform the guitar chords. The results showed that not just in the observation-to-imitate, but also during observation with no further requests and during observation no request to imitate, one saw activation of the inferior parietal lobule, the dorsal part of the PMv and the pars opercularis of IFG. However, the activation was much stronger when the subjects were tasked to imitate directly afterwards. In addition, one saw activation of the superior parietal lobule, anterior mesial areas and a slight activation of the middle frontal gyrus when subjects were asked to imitate directly after observation, but not otherwise.

In other words: the areas for new motor pattern formation, overlap with the mirror neuron regions (78).

**Single-neuron study in humans.** Though most studies of the mirror neuron system in humans have been indirect, recently one study was published in which extracellular single neuron activity in 21 patients with pharmacologically intractable epilepsy was recorded by means of an implanted intracranial electrode (used to identify seizure loci before a potential surgery). The activity of a total of 1117 neurons were recorded from medial frontal cortices and temporal cortices while the patients either observed (via laptop screen) or executed hand grasping (precision grip and whole hand prehension) and facial emotional expressions (smiling or frowning). In accordance with prior studies in monkeys, the majority of the studied neurons responded to only one aspect of a particular action, i.e. either execution or observation, but a significant subset responded to both were found in the medial frontal and the medial temporal lobe, specifically the hippocampus, parahippocampal gyrus and the entorhinal cortex. A further subset of these cells responded with excitation during action execution and inhibition during observation (79).

The finding of motor mirror neurons in the medial temporal lobe is fascinating. Though it is known that the uncinate fasciculus and other cortico-cortical white matter tracts connect between the medial temporal lobe and motor region in the frontal lobe (80-84), it is also known that lesions in the medial temporal lobe do not result in any apparent motor deficits, and electrical stimulation of the area does not result in any evident movement. However, the region has been shown to respond during the recall of episodic memory (79). On this basis, the authors of the study theorize that the mirror neurons in the medial temporal lobe may be matching the observed actions with the memory of the same action as performed by the observer - a memory presumably formed during the past execution of said action (79).

## Discussion

Since the first reported findings of mirror neurons in 1992 (2) there have been numerous studies verifying and refining the original discovery both in monkeys (1, 3, 25-27, 32, 51, 58) and in humans (5, 12, 56, 57, 63, 65, 66, 74, 79, 83), including an article detailing the direct study of single neurons in humans (79). Indeed, the author of this paper has been unable to find a single article written in the past 5 years that doubts the accuracy of these findings; the existence of mirror neurons is no longer in dispute. The debate over their functions however, is far from settled.

What follows is a discussion on the possible role of mirror neurons in action understanding, motor imitation, motor learning, and briefly their possible role in the evolution of language. Other fields in which mirror neurons might have a role, such as empathy, autism, stroke rehabilitation and phantom limbs will be briefly mentioned to provide the interested reader with easy access to relevant source material. An in depth look at these subjects is unfortunately beyond the scope of this paper.

**Action understanding.** That they play a role in action understanding was one of the earliest suggested functions of mirror neurons (3, 6). To quote Rizzolatti et al.: *"Each time an individual sees an action done by another individual, neurons that represent that action are activated in the observer's premotor cortex. This automatically induced, motor representation of the observed action corresponds to that which is spontaneously generated during active action and whose outcome is known to the acting individual. Thus, the mirror system transforms visual information into knowledge."* (1)

Evidence in support of this theory comes primarily from experiments in which the subjects have access to enough information to infer the goal or purpose of the observed action, but is unable to receive the full sensory stimuli needed to observe the full action itself. One example of this is an experiment in which a monkey was prevented from observing the final part of an action (grasping an object), but could see enough to infer the purpose of said action (the hand moving to grasp a hidden object which the monkey knows is present). Though the full action was not visible, the activation of the mirror neurons was just as strong when the object was present, while there was no response when the object was absent (26). Another experiment found that a subset of mirror neurons in a monkey's area F5 discharge both when the monkey executes an action and when it hears a sound that typically accompanies such an action, for example the crushing of a peanut (27, 28). Yet another experiment tasked monkeys to grasp an object by means of either regular or reverse pliers, one requiring the opening while the other required closing of the fingers to operate. The mirror neurons fired equally strong in both cases (30). Finally, in another experiment, human subjects were presented with still images of hand and mouth actions, for example the grasping of a bottle, i.e. only the idea of the action and the goal of the action was presented as stimuli, with no dynamic movement at all. The brain regions responded just as strongly as they would when observing the actual dynamic movement (77).

Criticism of the theory, has been mostly related to its rather vague formulation, that largely sidesteps the mechanics involved in favor of a more teleological explanation (85-87). After all, what does action *understanding* actually mean? What do mirror neurons actually decode? One way of categorizing this, is by levels of abstraction: Level 1: decoding the motor parameters of an action in detail, i.e. the path of a hand movement. Level 2: decoding the motor action at a schema level, i.e. picking up a peanut from a bowl. Level 3: decoding the goal or intention of the motor action, i.e. desires to eat a peanut. Note that level 3 deals with a more abstract representation, while the first two levels decode a motor code that basically reproduce the observed action, which can be very different from the intended effect of the action. This is precisely the scenario in the experiment involving normal and reverse pliers, where at the first and second level of abstraction, the action is opposite (opening and closing of the hand), while at level 3 it is the same in both circumstances. Since the mirror neurons fired equally strongly in both cases (30), it seems most likely that if the mirror neuron system do indeed decode motor actions, they do so at this third level of abstraction.

From the discussion above, it is fair to suppose that if the monkey indeed understands the action, then the mirror neuron activity is closely associated with this understanding. However, it remains unclear whether this understanding is caused by the mirror neuron activity or precedes it. It is also unfortunate that none of the mirror neuron experiments tested whether the monkey actually understood the actions it was observing, thus the foundation for the theory of action understanding is not as sound as one may desire.

As an example, recall an experiment described above, which showed that mirror neurons respond to the grasping of an object, even when the last part of that action is hidden from view, but do not respond if the monkey is shown that no graspable object is present behind the obscuring glass (26). This has led some to claim that it was when the monkey was shown the presence or absence of the graspable object that understanding took place, and before the firing of mirror neurons (88). However, I do not agree with this assessment. The findings of the above mentioned study, is in accord with another experiment which showed that the behavior of mirror neurons depends on the operational space of the subject, with some being distance specific and some changing their behavior from responding to action only in the peri-personal space to extra-personal space or vice versa, depending on the subject's available motor options (35). These results do not necessarily mean that the understanding process takes place elsewhere in the brain and that the mirror neurons merely report on it, as



some have suggested (88). Another equally possible, if not more likely, interpretation, is that the mirror neurons are part of a greater understanding network, and that mirror neurons probably cannot mediate action understanding by themselves.

Still, if the action is understood during the planning phase of an action, what then is the purpose of the mirror neuron firing? Certainly, it is not motor movement, since no such occurs when the mirror neurons discharge; though this is probably due to an inhibitory mechanism (34, 73, 79). One proposed explanation, called augmented competitive queuing (ACQ), is that they contribute to the monitoring of one's own success of self-action and to the recognition of one's own apparent actions. In short: when someone starts to execute a motor action, mirror neurons will, based on the given circumstances, create an expectation of reaching the goal of said action. If this goal is not reached, the brain will lower its estimate for the likelihood of said action succeeding in the future. If the goal is reached, regardless of whether the action was properly executed or not, the brain will increase the desirability of carrying out such an action again. In essence, the mirror neurons serve a "what did I just do?-function (89). What is especially intriguing about this theory, though the authors strangely do not mention this in their article, is that it is the only theory that properly explains the findings that mirror neurons prefer the 1st person perspective (45).

Another criticism leveled at the original theory of Rizzolatti et al. deals with how the subject assesses the success of a motor action. If one takes the experiment with pliers (30) as an example, how does the monkey know that the goal (grasping) has been achieved? Hickok postulates that this happens through the visually determined positioning of the pliers and the somatosensory stimuli (e.g. the resistance of the pliers), in other words: if the monkey was blindfolded and prevented from receiving somatosensory information, it would have no way of knowing if the action was successful. Thus, he postulates that the goals of an action lie in the consequences of the action, and these in turn are understood by perceptual systems, not motor systems (87). This has however never been tested, nor is it entirely logical, as the mirror neurons fire during the action, before the subject knows if the action was successful. Thus, perceptual systems are required to determine the goal of an action, and might be used to modulate future motor actions, but ignoring the motor aspects entirely appears to be unsound. Following the same logic as above, what use would a perceptual system be, if the subject had no motor repertoire and thus had no way of knowing how to achieve a particular goal, nor indeed what the various possibilities are in different conditions? It seems that a more logically sound argument would be closer to the one in the previous paragraphs, namely that both perceptual and motor systems are required for action understanding.

Still, it cannot be denied that there are other areas that are active during action perception. Notably, the STS region has been shown to respond to the observation of motor actions (90, 91), and when the function of this region is interrupted, either by rTMS (92) or degenerative disease (93), the subject's perception of biological motion and perhaps also action understanding is impaired. The results however are unclear, and difficult to interpret (94, 95). Further, there is nothing to suggest that the STS region is capable of generalizing over multiple body effectors, for example responding to both hand and foot, the way mirror neurons have been shown to do (58, 96). Nor is there anything to indicate that the STS region responds to both proximal (grasping an object) and distal outcomes (eating that object), as mirror neurons have been shown to do (42, 97, 98).

And so, we are left with that the most likely theory is that the mirror neuron system underpins action understanding: By recruiting one's own motor representation during the observation of a motor action, one is able to understand what the other is doing without any additional higher-order processing. It also seems likely that this is not something that is just viewed externally, as something that happens among others, but represented internally, as an outcome towards which one's own actions can be directed. This is based on the findings

showing that the greater the observer's own motor repertoire, the better that person is at identifying the outcome of someone else's actions (99-103). Further, it has been shown that patients suffering from limb apraxia due to brain damage of the left inferior frontal cortex (part of the frontal node of the mirror neuron system), struggle to identify gestures performed by others (104). Likewise, virtual lesions of the left premotor cortex have been shown to result in patients struggling to discriminate both static (105) and dynamic (106) bodily actions, as well body postures (107). In addition, both behavioral (108) and electrophysiological (98) studies have shown that subjects that struggle to represent distal outcomes of one's own motor actions, likewise struggle to represent the distal outcome when observing actions, but not when executing them. This might suggest that action understanding specifically is impaired in these subjects.

Finally, multiple fMRI studies have shown that when human volunteers are tasked with determining to which outcomes (proximal vs. distal) an observed action is directed, the mirror mechanism is recruited (109-111). However, when the volunteers are tasked with determining the reasons why someone performed the observed actions, the mesial frontal cortex, the temporo-parietal junction and the anterior cingulate cortex (the so-called "mentalizing network") are additionally recruited (112). To what extent, if any, the mirror neuron system is capable of decoding not just the intention of actions, but also the reasons behind the actions, e.g. desires, beliefs, etc., remains unclear. Likewise, how this "mentalizing network" might work and interact with the mirror neuron system, is equally unknown.

**Imitation.** Various psychological experiments strongly suggest that stimuli and responses to them are represented in a comparable format in the cognitive system. When an individual observes a motor movement that is similar to one in their own motor repertoire, the observer is primed to repeat it; and the greater the similarity, the stronger the priming (113-116). Thus, it is easy to understand how the discovery of mirror neurons prompted many to believe that they serve as the neural substrate for imitation (1, 7-12). Several fMRI experiments have shown that imitation specifically activates the pars opercularis of the IFG, the anterior parietal region, the parietal operculum and the STS region (10, 12). Broca's area has also been found to be important to imitation (11), particularly when the action is goal-related (9). Mouth movements have also been studied in a similar fashion with similar results (8).

These findings show that the brain regions that are active during motor imitation and during action observation overlap, and these areas are known to have mirror neuron properties (56). More compelling evidence of these region's involvement in imitation specifically, comes from an experiment in which pars opercularis was incapacitated by means of rTMS in human subjects, during either the imitation or spontaneous execution of finger button presses. Imitation was severely impaired, while the spontaneous execution was seemingly unaffected (7).

Still, all of these experiments are on a regional level, and we know that only a subset of the cells in the given region are known to have mirror neuron properties. How much of these results are due to the functions of mirror neurons specifically is therefore difficult to assess. Furthermore, monkeys have been largely believed to be incapable of imitation (117, 118), leading some to claim that, at least the primary role of mirror neurons cannot be imitation (1). However, research of the past few years has complicated matters quite a bit: neonatal rhesus monkeys have been shown to imitate human tongue protrusion and lip smacking (119), and, once taught to share attention with humans via eye gaze or pointing, they will imitate other actions as well, such as clapping hands, touching their own ears and clenching their hands (120). It therefore seems that the early dismissal of some scientists of the role of mirror neurons in imitation was premature. However, it has repeatedly been shown that mirror

neurons respond to the goal of an action rather than the movement used to achieve it (6, 26, 30, 42, 58), while motor imitation is obviously dependant on the manner in which the movement is made. Though the human mirror neuron system does respond to intransitive movements (56), it seems unlikely that humans have evolved an entirely separate method for imitation than monkeys have.

Based on the above, it is unclear whether mirror neurons play a role in motor imitation, and if they do, it is equally unclear what the specifics of that role would be. Research on this subject is still at an early stage, and no consensus has yet been reached.

**Evolution of language.** Almost immediately upon the discovery of mirror neurons (2, 3, 6), they have been used as evidence in support of the gestural theory of the evolution of language, i.e. that language evolved from motor gestures rather than primate calls (18). This theory is far from new; as early as the 1930s scientists suggested that the act of pointing evolved from observing children grasp far away objects (121). Others have suggested that speech perception is not based on sounds but rather on phonetic gestures of the speaker. These phonetic gestures act as the primitives from which actual articulatory movements are produced (122-125). For example, if the mouth, tongue and lips move as if one is eating this can be interpreted to mean "eating" (phonetic gesture), and if one blows out air to produce a sound similar to "mnyum" - while making these movements, it is seemingly universally understood, even by children (126).

Some have suggested that the mirror neuron system serves as the neural substrate for speech perception (3). This is partially based on the generally agreed upon assumption that Broca's area in humans is the homologue of the monkey's area F5 (1, 57, 58). The existence of auditory mirror neurons (27, 28) shows that there also exists mechanism for representing sounds as motor gestures. Furthermore, the human mirror neurons system, unlike that of monkeys, also responds to intransitive movements (69-71), theoretically allowing the understanding purely symbolic or communicative acts (69). This is especially interesting, since language is considered to be an ability relatively unique to humans (127-129). Moreover, the language areas of the human brain map remarkably close to the mirror neuron system of the primate brain (130). Finally, it has long been a clinical fact that aphasic patients often struggle to recognize pantomime (131-134). Though some have suggested that this is due to a concomitant lesion of an area adjacent to Broca's area (135), it is tempting to suppose that this is not the case, since this is precisely the kind of deficit one would expect from the reasoning above (3).

Though this is still a hotly debated topic, it is becoming increasingly likely that mirror neurons do in fact play some role in the evolution of language. For an excellent review of the subject, the interested reader is encouraged to read the work of Corballis (18).

**Autism.** Upon the realization that some of the symptoms associated with autism spectrum disorder (ASD), i.e. the capacity to understand others, difficulties with language and communication, overlap with some of the proposed functions of mirror neurons, the hypothesis that the core of ASD was a mirror neuron system deficiency was put forward (19, 20). Early fMRI and TMS studies appeared to support this theory (136), but lately reviews and meta-analysis have changed this view. The imaging studies that used emotional stimuli did show group differences between autistic and non-autistic subjects, but when using non-emotional stimuli no such differences were shown. Neither has it been possible to consistently demonstrate that autistic subjects struggle with action understanding (137, 138). As of now, it remains unclear whether a dysfunction in the mirror neuron system plays a role in ASD.

**Empathy.** The research on the role of the mirror neuron system in empathy is still in its early stages. It appears as though mirror neurons in the human insula might be responsible

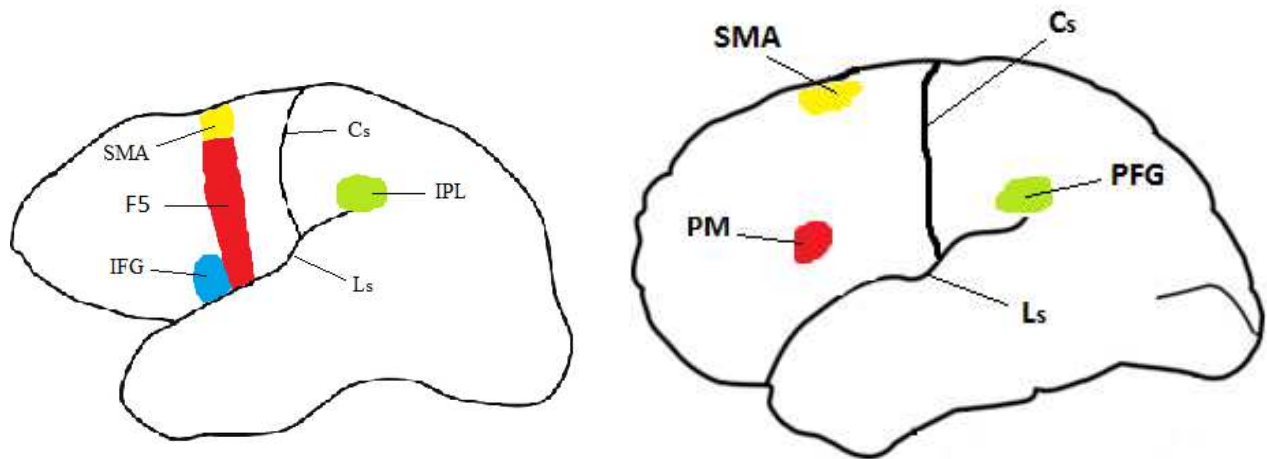
for the recognition and understanding of disgust in others (139, 140), however there appears to be little in terms of other concrete findings. More theoretical reasons may be found in Häusser's excellent review (141), and for a more critical review of the subject, the interested reader is encouraged to peruse a review by Baird et al. (14)

**Stroke rehabilitation.** A few studies have been published, attempting to assess the possible use of action observation and imitation as part of stroke rehabilitation treatment, attempting to harness the mirror neuron system in a clinical setting. Early results are mostly positive, however not all studies conducted had a satisfactory control group, and the overall picture is mixed (15-17). This research is encouraging, but at an extremely early stage, and no conclusions can be made as of yet.

## **Conclusion**

The existence of mirror neurons is no longer in dispute. It is likely that the mirror neuron system underpins action understanding, as part of a greater cognitive network. It is unclear whether mirror neurons play a role in motor imitation, and if they do, it is equally unclear what the specifics of that role would be. It is becoming increasingly more likely that mirror neurons have played a role in the evolution of language, though the topic is still hotly debated. The research on the role of the mirror neuron system in other fields, such as autism, empathy and stroke rehabilitation is still at too early a stage to draw any conclusions. Early results are discouraging for their role in autism, and encouraging for their potential in stroke rehabilitation.

## Attachment



**Fig. 1.** Simplified illustration of brain regions believed to be part of the mirror neuron system of monkeys (left) and humans (right). PM, premotor cortex; SMA, supplementary motor area; IPL, inferior parietal lobule; F5, rostral part of the ventral premotor cortex in the monkey; IFG, inferior frontal gyrus; PFG, rostral part of the inferior parietal lobule; Cs, central sulcus; Ls, lateral sulcus.

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