

Mirror Neurons: Findings and Functions

REVIEW

Mirror neurons (MNs) are a set of premotor neurons that fire both during the performance of a motor action, and the observation of someone else performing the same action. Since their discovery, they have been the subject of great controversy. This survey provides a short overview of the history and the most important findings of MN research in animals and humans. Special focus is given to the latest findings on empathy and relevant disorders i.e. autism, schizophrenia and psychopathy, in the context of MNs. Finally a review of the criticism on MNs is provided and discussed.

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INTRODUCTION

The human brain consists of countless neurons and neuronal connections, each one distinct in locality and function within the network. It contains neural circuits for all the types of behaviours included in the human repertoire, e.g. comprehension, attention, recollection, daydreaming etc. However, there is one group of neurons that has been a source of huge excitement, as well as great debate since its discovery, i.e. Mirror Neurons (MNs).

Di Pellegrino, Fadiga, Fogassi, Gallese and Rizzolatti (1992) found coincidentally some neurons in the macaque monkey brain that had the distinct properties not only to fire when the monkey was performing an action, but also when it observed someone else performing the same action. These neurons were named mirror neurons because they were able to mirror the observed behaviour. Specifically, they fired as if the observer himself was executing the observed action.

An important point to make is that MNs should be differentiated from

canonical neurons that reside in the same areas. Both are visuomotor neurons but have distinct properties. Canonical neurons fire when a goal-directed movement is made and when the object related to that movement is observed. On the other hand, MNs also fire when a goal-oriented movement is made, their additional property is firing when someone else is observed doing the exact same movement (Tummolini, Castelfranchi, Pacherie & Dokic, 2006).

MNs are mainly located in the F5 area of the premotor cortex of the macaque brain (di Pellegrino et al., 1992). Initially the research focused on animals, e.g. it was discovered that the monkey's MNs play a vital role in action understanding (Umiltà et al., 2001; Kohler et al., 2002). The findings of animal research have set the basis for the research of MNs in the human brain. There is a large amount of literature stating that the human MNS contributes to the evolution of language in humans (Rizzolatti & Craighero, 2004), imitation (Ramachandran, 2000; Oztop & Kawato & Arbib, 2006; Iacoboni, 2005), empathy (Gallese, 2001) and Theory of Mind (ToM ; Gallese & Goldman, 1998). However, other findings suggest that the MNs are just a simple reaction to an observed stimulus without any action-understanding (Hickock & Hauser, 2010). Some other research even suggests that MNs do not exist in humans at all (Turella, Pierno, Tubaldi & Castiello, 2009).

This review surveys the most important findings on MNs. The first section presents and discusses findings concerning MNs in animals, followed by a section on human MNs. After that, research on the relation between empathy and MNs is discussed, along with recent findings in the domain of psychopathology in combination with the MNs. The article concludes with a discussion on the findings, including some of the most important criticism on the MNs, and some final thoughts on potential future research directions.

FINDINGS IN ANIMALS, THE DISCOVERY OF MN'S AND BEYOND

In 1992 Di Pellegrino et al. investigated area F5 of the macaque premotor brain area. The initial purpose of their study was to differentiate between brain activity induced by presented stimuli and activity related to movements, using single cell recordings. For this technique, micro-electrodes are placed in or near the cell membrane of a neuron, allowing the recording of the activity and the temporal discharge of individual neurons in response to a stimulus (Boulton, 1990). Single cell recordings are therefore a very useful tool for measuring neural activity directly.

By accident, the aforementioned researchers discovered something very interesting: apparently, neurons in the F5 area were activated when the monkey simply observed the experimenter performing a motor action. The researchers focused on investigating this phenomenon further by recording F5 neuron activity during execution and observation of motor actions. These actions were basic motor actions included in the monkey's repertoire, such as actions related to food grasping, the manipulation of objects, and gestures. As expected, almost all of the measured neurons in the F5 area fired when the monkey performed a motor action. Interestingly, the majority of the neurons also fired when the monkey observed a motor action.

After the first experiment, a great amount of research has provided evidence for the location of the MNS and its properties. This research has shown that there appear to be other areas with mirror properties. Besides the premotor area, one of its important input areas, the rostral inferior parietal lobule (IPL) area PF, also contains neurons with mirror properties. The premotor area and the PF are highly interconnected. Most of the PF neurons (90%) respond to visual stimuli, but only half of these neurons are also active during motor actions. The PF sends output to the F5 area and receives input from the superior temporal sulcus (STS; Rizzolatti, 2004). The STS is comprised by visual neurons, which respond to observed biological actions, such as moving faces or bodies (Puce & Perret 2003). Moreover, the STS plays a role in gaze perception and is therefore important in understanding others' direction of attention (Campbell, Heywood, Cowey, Regard & Landis, 1990). Even though the STS has no motor properties and is not considered to be a part of the MNS it is highly involved in the functioning of the mirror neuron system via its connections with inferior parietal parts of the MNS. To conclude, it can be said the cortical MNS in monkeys constitutes the ventral premotor area and the rostral inferior parietal lobule (Rizzolatti, 2004).

More recent research has shown that some neurons can only be activated by observation of very specific motor actions, whereas others fire if the monkey observes motor actions that achieve a similar goal. This led to the conclusion that different types of MNs exist: the strictly congruent MNs (the former) and the broadly congruent MNs (the later). Broadly congruent MNs are higher in quantity than the strictly congruent, occupying approximately two thirds of the MN population (Iacoboni & Mazziotta, 2007).

FUNCTIONS OF MIRROR NEURONS IN ANIMALS

One of the hypothesized functions of animal MNs is to aid understanding the intention of an observed motor action, as already hypothesized by Di Pellegrino et al. (1992). They found the firing of MNs did not depend on a specific object involved in the motor action or on a specific motor gesture, but on the meaning or intention of the action. Therefore the authors hypothesized that MNs are important for the automatic understanding of goal directed behaviour.

Additional research has provided support for this claim: MNs have the ability to fire for goal directed behavior even when an object is partially hidden. This was found in monkeys (Umiltà et al., 2001). Moreover, studies have demonstrated the existence of audiovisual MNs in the monkey premotor area, besides the visual based MNs. This type of neurons has the ability to fire when the animal performs an action and when it hears a sound that is related to that specific action (Kohler et al., 2002).

Further research into the F5 area of the monkey's premotor cortex, specifically the ventrolateral premotor cortex, has demonstrated that the MNs located there fire during the observation of actions made with tools, the so called tool - responding MNs. These neurons fire when the monkey makes a hand or mouth movement, but also when the researchers manipulate a tool.

These neurons are congruent, with the sense that their aim, when they fire, is a manipulation of an object, observed or executed (Ferrari, Rozzi & Fogassi, 2005). Another interesting finding is that one third of the mirror neuron population in area F5 fires when the monkey observes mouth actions. These “mouth mirror neurons” fire when the observed movements are related to ingestive functions, but fire more prominently during communicative gestures, e.g. lip smacking. This may underline the importance of the MNs in communication. Interestingly, in humans the homologue of the F5 area is Broca’s Area, an area highly involved in language. This could have further implications on how language evolved in humans (Ferrari, Gallese, Rizzolatti & Fogassi, 2003).

Moreover, in a study using single cell recordings researchers measured the activity of the F5 neurons when the action was performed at different distances from the monkey. They found that 26% of the premotor neurons fired when the observed movement was made in the monkey’s extrapersonal space, 27% when in the peripersonal, and 47% fired independently of location, in which the observed movement was executed. This indicates that observed actions executed at different distances from the monkey are differently encoded by MNs. These findings have potentially strong implication for social – and potentially human - behavior, since in a social environment is it important to quickly respond to observed behavior based on its location relative to the observer (Caggiano, Fogassi, Rizzolatti, Their & Casile, 2009).

To summarize, animal research has demonstrated that MNs encode an action differently, dependent on the locality with respect to the observer and that MNs fire when the monkey observes mouth movements, when it observes actions made by tools or motor actions that are present in its repertoire.

THE HUMAN MIRROR NEURON SYSTEM

In the past decade, a considerable amount of research has been done into the human MNs. Besides the main function of goal understanding, the human MNs are often endowed with other functions, such as imitation, language acquisition, and emotion (Fabbri-Destro & Rizzolatti, 2008).

Techniques used in humans to study MNs

Although single cell recordings are very useful for the study of MNs, they are rarely found in human research since they can only be performed when a patient requiring the insertion of intracranial electrodes agrees to participation in an experimental study (Engel, Moll, Fried, Ojemann, 2005). Before discussing results from human research, it is important to describe briefly the techniques most commonly used in human research for MNs.

Transcranial Magnetic Stimulation (TMS) is a noninvasive technique that is widely used to study MNs in humans. A TMS-device induces a powerful electromagnetic field capable of depolarizing superficial neurons (current max range from brain surface: 2mm), thereby causing these neurons to initiate action

potentials (Pascual-Leone, Davey, Rothwell, Wassermann & Puri, 2002). Research has shown that when single or paired pulse TMS is applied to the human motor cortex, it causes a temporary increase in cortical motor excitability (Nitsche & Paulus, 2001). This increase induces contralateral muscle activation called Motor Evoked Potential (MEP), which can be measured from these muscles by electromyography (EMG; Pascual-Leone, et al., 2002). Research shows that when we observe an action, there is a minor, sub threshold increase in activity in the muscles involved in that action, which is most likely caused by MNs (Cattaneo et al., 2009). Because this minor muscle activity can lead to MEPs, TMS is a useful tool to study MNs.

Besides single or paired pulse TMS, it is also possible to stimulate areas using repetitive TMS pulses (rTMS). This leads to longer lasting effects than ordinary TMS. Depending on frequency and the intensity of stimulation, rTMS can excite or inhibit areas (Fitzgerald, Fountain & Daskalakis, 2006). This way it is possible to create temporary, virtual 'lesions' in human subjects and investigate the functioning of specific brain areas by inhibiting these areas.

Another way of measuring MN activity is through encephalography (EEG). It has been observed that when humans are at rest, there is an 8-13Hz oscillation generated in the sensorimotor cortex. This is called the mu rhythm. When humans observe another individual performing an action, the neurons in the sensorimotor area fire asynchronously, causing a reduction in the mu amplitude. This is named mu suppression and it is considered to be an index of the MN activity (Ulloa & Pineda, 2007).

An additional technique used in human MN research is Functional Magnetic Resonance Imaging (fMRI). fMRI measures changes in cerebral blood flow. Increased neuronal activity leads to higher cell metabolism, which in turn leads to an increased cerebral blood flow in the activated area. fMRI can spatially pinpoint a rise in blood flow to precisions of up to a mm (Huettel, Song, & McCarthy, 2009). Since it has a good spatial resolution, it can be used to measure indirectly neuronal activity in very specific areas. Of course, findings from fMRI and EEG should be interpreted with caution, since there is no direct evidence that the measured activity really stems from the exact same type of MNs as the ones identified in monkeys with single cell recordings. We can assume it is the MNs firing based on function and location deduced from animal research, but unless single cell recordings are combined with fMRI or EEG we cannot say with certainty that the measured activity belongs to the MNs (Rizzolatti & Craighero, 2004).

Location

In humans, two mirror neuron systems have been identified by brain imaging studies. The first one is situated in the parietal lobe, the premotor cortex and the pars opercularis. The pars opercularis, also called Broca's Area, includes the IPL and the caudal part of the inferior frontal gyrus (IFG) and is a vital area for language. The parietofrontal network is responsible for the recognition of voluntary behavior. Since MNs are largely based in the motor cortex, it is not surprising that just like these motor areas, the MN show a somatotopic organization (Buccino, Binkofski, Fink, Fadiga, Fogassi, Gallese, et al., 2001; Marieb & Hoehn, 2007). The second MN system comprises the insula and the anterior mesial cortex. The limbic mirror system, as it is called, is endowed with the recognition

of affective behavior (Cattaneo & Rizzolatti, 2009; Fabbri-Destro et al., 2008).

One study that used single - cell recordings in humans, found that MNs are sparse in multiple brain areas. Specifically, they placed electrodes in the medial frontal and temporal cortex in patients suffering from epilepsy. These patients had to execute or observe hand actions and facial expressions. They found that a significant population of the neurons in the supplementary motor area and hippocampus fired both when they observed and executed actions (Mukamel, Ekstrom, Kaplan, Iacoboni & Fried, 2010). This suggests that besides the above mentioned main systems, additional areas in the human brain may have mirror properties.

Findings and Functions

The first study to report the existence of MNs in the human brain was a TMS study by Fadiga, Fogassi, Pavesi and Rizzolatti (1995). By applying TMS over the motor cortex they found increased MEPs when the participants viewed the experimenter performing hand movements, compared to control conditions. Since then TMS has provided ample evidence for the existence of MNs in humans.

Aziz-Zadeh, Maeda, Zaidel, Mazziotta, and Iacoboni (2002) tested the cortico-spinal excitability when the subjects viewed actions performed either by a left or a right hand, or a control stimulus during left or right motor cortex TMS. When TMS was applied to either the left or right motor cortex, MEPs increased during observation of a contralateral hand stimulus. These results indicate that human MNS fire automatically at the sight of a moving biological agent, like a hand, even in the absence of any motor output. Additionally, these studies indicate that the human brain, just like that of the macaque monkey, possesses neurons that fire during action observation and motor output of that same action.

Research supports the notion that the human MNS is also capable of encoding action intention. Buccino et al. (2004) in an fMRI study showed that motor actions that were in the participants' repertoire (e.g. a dog or a monkey biting something) activated the inferior parietal lobule and the pars opercularis, which are assumed to be part of the Mirror Neuron System, despite the fact that these actions were executed by animals. But when the action was not a typical human behavior, like barking, only visual regions were activated. This demonstrates that the human Mirror Neuron System is activated when an action, that is typical of human behavior, is observed no matter who is the agent of that action. More specifically, this experiment suggests that human MNs fire according to the intention of the action (dog/ monkey - biting), and not just the simple observation of the action itself.

This is further supported by an EEG experiment by Ulloa & Pineda (2007) in which mu suppression was measured. The authors used EEG to show that MNs are capable in deducing actions from sporadic, but meaningful visual input. They used point - light biological animation videos showing either biological human motion, matched scrambled version of this biological motion, or visual white noise. It was found that mu suppression was increased when the participants watched human movement, compared to the other two animations. These findings support the claim that human MNs have a key role in understanding human movements, even based on fragmented visual input.

Another area of the human MNs that has attracted attention is the inferior

frontal gyrus, which includes Broca's Area (Fabbri-Destro & Rizzolatti, 2008). Research has linked it with social perception (Keuken, Hardie, Dorn, Dev, Paulus, Jonas, et al., 2011) and action observation and imitation (Molnar-Szakacs, Iacoboni, Koski & Mazziotta, 2005).

Heiser, Iacoboni, Maeda, Marcus & Mazziotta (2003) investigated how essential the IFG is in imitation, using repetitive TMS to inhibit the area. In every trial, two sets of five pulses were applied with a rate of 5Hz to the left and right pars opercularis of the IFG. The results showed that inhibition of these areas by rTMS decreased performance on imitation tasks compared to control tasks, whereas inhibition of control areas (occipital areas) did not. This experiment shows the importance of the MNS, specifically the IFG in imitation behavior. The authors also concluded that Broca's area also plays a role in imitation, being a part of the IFG.

This evidence, that the MNs have a central role in imitation plus the observation that they overlap with Broca's area, a key language area in the human brain (Iacoboni & Dapretto, 2006) has led some to suggest the MNs might be involved in language evolution in humans. Rizzolatti et al. (2004) proposed a theory about this relationship. They suggest that gestural communication embodies meaning, which evolved to simple noises in the beginning and to complex speech later by the imitation capability of our MNs. MNs firing in response to auditory meaningful stimuli have been proven to exist in monkeys (Kohler et al., 2002).

To assess whether the human MNS could also be activated by auditory stimuli Lahav, Saltzman and Schlaug (2007) performed an fMRI study. In this experiment, subjects learned to play a new tune on the piano, which was later played back to them. During both playing and the listening session fMRI data were acquired. They found that the bilateral frontoparietal motor-related network, including Broca's area, was activated during the auditory perception of the newly acquired tune and during its execution. This system, which the authors named the hearing- doing system, depends on the subject's motor repertoire. Newly learned motor acts can be established in this network very quickly, as shown by the activity induced by listening to the newly learned tune. Moreover, this system has Broca's area as a hub. The authors therefore underline that this system might have important implications in language acquisition, as this hearing- doing system serves as an important sensorimotor feedback during speech.

Finally, MNs have been implicated in social interaction. In a study by Oberman, Pineda & Ramachandran (2007) showed that the MNS may play a role in social interaction. Mu suppression in response to four different movies was measured: a non-interacting, non-social movie (Non Social); non-interacting, social (Social Spectator Role); interacting, social (Social Interactive Role); and a control movie (visual white noise). The results were highly significant: the movie which induced the Interactive Role led to the highest mu suppression ($M = -.22$), followed by the Spectator Role movie ($M = -.15$). The non - social movie led to the lowest mu suppression ($M = -.08$). These results indicate that the human MNS can encode stimuli with social relevance.

In conclusion, it has still not been directly determined whether the MNs found in humans are of the same type as the animal MNs. However, the studies in humans have provided a great quantity of evidence which makes it safe to assume that neurons with mirror properties at least seem to exist and that these proposed

MNs have implications in action observation, intention understanding, imitation, social interaction and their potential role in language evolution. Besides these implications, the MNs have also been associated with empathy.

MIRROR NEURONS AND EMPATHY

One of the most important implications of the MNS in humans is its importance in empathy. Some theories suggest that the functioning of the frontoparietal mirror neuron system is vital for the understanding of other people's emotions, implying that dysfunctions may impair empathy.

Empathy is a very broad term, often used in the human sciences, from philosophy and sociology, to psychology and now to neurosciences. This wide usage of this term is the reason that it has multiple definitions, dependent on the perspective one takes. One satisfying definition is that: empathy is "a mechanism for inferring and experiencing, what another feels by simulating it through a shared self- other representation" (Pineda, Moore, Elfeinbeinand & Cox, 2009).

In order to explain its neural mechanism, Blair (2005) suggested that there are three forms of empathy: emotional, cognitive and motor empathy. According to Blair, MNs can account only for the motor empathy of humans, which most importantly includes imitation. Cognitive empathy arises from temporoparietal regions (regions associated with ToM), while emotional empathy depends mainly on limbic regions. All three kinds of empathy interact with each other in order for the individual to be fully empathic. Nevertheless, in this view, the MNs are given a more primitive, purely motor and rather simple form of empathy.

Two other main theories are Theory - Theory (TT) and Simulation - Theory (ST). TT states that individuals can infer the emotional state of another by relying on common theories about behavior or emotion, also known as folk psychology. ST on the other hand, states that in order to understand another person's state, an individual must place oneself in the other person's shoes to know the other person's feelings (Gallese et al., 1998).

Proponents of the ST view suggest that the MN gives humans the ability to simulate other people's intentions and emotions by the mere observation of another individual. It has been found that observation of emotional expressions activate our MN circuit, which can then evoke feelings similar to those observed (Gallese et al., 1998; Kaplan et al., 2006; Gallese, Eagle & Migone, 2005).

Finally, another view states that MNs are the neural substrate of ToM. ToM is closely related to empathy and has its roots in philosophy. It proposes that people have the knowledge that mental or emotional states are different among individuals and are able to acknowledge them. These inner states can be emotions, goals, perspectives, knowledge, etc. (Agnew, Bhako, & Puri, 2007). Research has shown that ToM is clearly dysfunctional in people with Autism Spectrum Disorder (ASD; Baron-Cohen, Leslie & Frith, 1985). Moreover, research has shown that people diagnosed with ASD have dysfunctional MNs (Williams, 2008). This is why some researchers believe that dysfunctional MNs may be one of the main causes for autism (Rizzolatti et al., 2009).

IMPAIRMENTS IN MIRROR NEURON SYSTEM AND SOCIAL DISORDERS

Autism

The link between MNs, ASD and empathy has been researched extensively and the “broken mirror” hypothesis has been researched by Oberman. In their study, Oberman et al. (2005) found that MNs are dysfunctional in highly functioning individuals with ASD. In this experiment the subjects watched four different videos showing a moving hand, a bouncing ball, visual noise or a movement of their own hand. They found a lack of mu suppression in the sensorimotor cortex of ASD patients, compared to unimpaired controls, during the first and fourth condition. The authors state that although ASD patients showed normal mu suppression during hand movement, they failed to show any during both conditions of hand movement observation, which indicates a dysfunction in the MNs. Moreover, they propose this finding may also be related to the deficits ASD patients show in imitation and ToM.

Support for the above finding is provided by Williams et al. (2005) who showed in an fMRI study that patients with ASD have an impaired MN circuit activation. In their experiment participants had to execute movements with their fingers directed by a symbolic cue or imitate the same actions by watching pictures of fingers. They found that although participants with ASD activated their MN circuit in the anterior parietal area, they did so to a lesser extent than controls in the second condition. Moreover, the patients showed less activation than expected in the somatosensory cortex and no modulation of the left amygdala during imitation. This led the researchers to hypothesize that patients with ASD may still have the primary function of imitation intact. However, their MNS may not be capable enough to skillfully employ empathy and ToM.

Another view proposes that the parietofrontal MNs is highly connected with the limbic MNs, which may provide a system sufficient for understanding the emotion of others (Cattaneo et al., 2009). The limbic system is known for its implication in emotional situations (Isaacson, 2001). The proposed MNs-limbic network comprises the frontal MNs, the insula and the amygdala and it is thought to facilitate the understanding of others’ emotions through action representation. This system is found to be dysfunctional in people with autism and this dysfunction is thought to be responsible for the lack of empathy and social understanding (Dapretto et al., 2006; Iacoboni, 2005).

To conclude, most of the evidence suggests that MNs are dysfunctional in ASD patients. However, based on the available literature it cannot be concluded whether there is a causal relation between a dysfunctional MNs and ASD, or whether dysfunctional MNs are the result of other symptoms related to ASD.

Schizophrenia

Schizophrenia is a psychotic disorder with a mixture of positive symptoms (such as delusions or hallucinations) and negative symptoms (such as affective flattening, alogia and avolition; DSM-IV-TR, 2000). How is this disorder related to the malfunction of the MNs? Arbib and Mundhenk (2005) proposed that the malfunction of the MNs is associated with the positive symptoms of schizophrenia,

especially hallucinations, because schizophrenia patients are not able to identify the generation of thoughts or actions as their own.

In one study, schizophrenia patients could not discriminate their own hands from someone else's, stating sometimes that the foreign hand was their own (Buccino & Amore, 2008). This led Arbib and Mundhenk to suggest that these patients had impaired self-monitoring. This impairment was associated with an inability to effectively recruit the MNs, which was potentially caused by a deficit in working memory. Specifically, they suggested that the patients could not form memory traces of their own actions. This, in turn, led to a decreased recruitment of their MNs. This may be a reason for attributing the initiation of their own actions to others. Although MN deficit does not have a primary role in schizophrenia, it is proposed that it is a result of working memory dysfunction.

Psychopathy

Psychopathy is defined as the inability to feel what others are feeling along with the characteristic to manipulate people (Blair, 2005). To date only one study investigated the direct link between MN activity and psychopathic traits.

Fecteau, Pascual-Leone & Théoret (2007) conducted a study in a non-psychiatric sample, where they investigated MEPs using TMS. The participants watched four different videos: a static right hand; a needle penetrating the skin of a right hand; a needle penetrating a fruit; and a cotton stick touching a hand. TMS pulses were delivered at two different time points: in the short condition the TMS pulse was delivered one second after the film started (before needle/stick penetrates/contacts object); in the long condition, three seconds after the beginning of the film (during penetration/contact).

Results from MEPs in the long condition were correlated with scores on the Psychopathic Personality Inventory (PPI). The results indicated that people with higher levels in the cold-heartedness scale of the PPI, showed greater MEP reductions while viewing the video penetrating the hand (emotional video), compared to participants with lower scores on that scale. As cold-heartedness is considered a gold standard for the diagnosis of psychopathy, this finding suggests that people with high scores on psychopathic traits show less motor empathy in response to observed pain than control subjects. Even though the only experiment so far investigating the relation between MNs and psychopathy only investigated psychopathy traits in a non-psychiatric sample, it seems to indicate that there may be a relation between psychopathy and dysfunctional MNs.

DISCUSSION

The MN discovery has been characterized by many as the most prominent discovery of the past decades. Ramachandran (2000) said: "I predict that mirror neurons will do for psychology what DNA did for biology: they will provide a unifying framework and help explain a host of mental abilities that hitherto remained mysterious and inaccessible to experiments". But more than a decade after their discovery: did they

really explain these mysterious mental abilities? And is there even a consensus about the existence of MNs in humans?

Do We Have Mirror Neurons?

From the MN experiments, the majority does not concern experiments on humans, but on monkeys (Pascolo, Ragogna & Rossi, 2009). MNs were first found in monkeys using single cell recordings (Di Pellegrino et al., 1992). Until single cell recordings are combined with fMRI or EEG we cannot say with certainty that the measured activity in humans belongs to the same type of MNs found in monkeys. Even one of the researchers who originally found the MNs states in his article that direct evidence of MNs in humans is still missing, only indirect evidence has been obtained (Rizzolatti et al., 2004). There have been no adequate studies to certify that MNs similar to those found in monkeys really exist in the human brain. So far a To what degree the exact location of these neurons corresponds to animal areas and other areas identified in human MN research remains to be seen.

What Mental Abilities Can Mirror Neurons Explain?

Like in monkeys, research has associated the proposed human MNs with action understanding (Buccino et al., 2004). Besides this basic ability, other implications of MNs in humans are imitation (Ramachandran, 2000; Oztop & Kawato & Arbib, 2006; Iacoboni, 2005), language acquisition (Rizzolatti & Craighero, 2004), empathy (Gallese, 2001), and ToM (Gallese & Goldman, 1998). Furthermore, MNs dysfunctions have been implicated in social disorders, like autism (Oberman et al., 2005), schizophrenia (Arbib and Mundhenk, 2005) and psychopathy (Fecteau et al., 2007). However, whether there is a causal relationship between the MNS and the disorders is not entirely clear and requires further research.

Future Research

Most importantly, to bridge the gap between animal and human findings and to establish whether MNs in humans are the same type of neurons as the ones found in animals, single cell recordings should be combined with imaging techniques like fMRI and EEG either in humans or animals. This way human MN research will have a stronger scientific foundation than the indirect evidence and assumptions it is mainly based on now.

Also, future research on the MN topic should focus on clearly defining and accurately localizing the mirror neurons in humans. Currently, not all studies agree on the exact subareas of the MNS involved in certain types of behavior. For instance, a meta-analysis was conducted on fMRI studies for the implication of MNs in imitation. They identified the inferior parietal lobule and the dorsal part of the premotor cortex as areas systematically involved in imitation. The role of the pars opercularis and the frontal area, which are cited to be crucial for imitation by other researchers, were questioned by this meta-analysis (Molenberghs et al, 2009).

Some MN studies in humans show methodological limitations: brain activity was not always measured during both observation and execution (e.g.: Saltzman

and Schlaug, 2007; Ulloa & Pineda, 2007). In most of the experiments the subjects were instructed just to observe an action and not to execute it. This is a limit, since it identifies only the area responsible for observation of an object or action, which may differ from the area responsible for execution as well as the observation (Turella et al., 2009). It is important that the study of MNs is oriented towards populations that have deficiencies in ToM or empathy, for instance people diagnosed with ASD, schizophrenia or psychopathy. It should be investigated if the MNs dysfunction in such cases is a side effect from another abnormality or the main factor of the disorder. The clinical applications, if found, should be consolidated and expanded.

Closing Remarks

The criticism on the MNs from its rivals is as robust as the enthusiasm from its followers. In the past decades, perhaps no discovery has given more expectations to the psychological community than the MNs. However, the mirror neurons and their potentials do not yet rest on solid ground and still remain a mystery. We hope future research will be able to clarify the main uncertainties, discard the inconsistencies apparent in some of the MN findings and lead to more insight in the role of the MNs.

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