BRAIN RESEARCH REVIEWS

Review

The human mirror system: A motor resonance theory of mind-reading

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ABSTRACT

Electrophysiological data confirm the existence of neurons that respond to both motor and sensory events in the macaque brain. These mirror neurons respond to execution and observation of goal-orientated actions. It has been suggested that they comprise a neural basis for encoding an internal representation of action. In this paper the evidence for a parallel system in humans is reviewed and the implications for human theory of mind processing are discussed. Different components of theory of mind are discussed; the evidence for mirror activity within subtypes is addressed. While there is substantial evidence for a human mirror system, there are weaknesses in the attempts to localize such a system in the brain. Preliminary evidence indicates that mirror neurons may be involved in theory of mind; however, these data by their very nature are reliant on the presence, and precise characterization, of the human mirror system.

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Contents

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1. How can cognition emerge from neurons?

A major aim of cognitive neuroscience is to explain how the brain functions in terms of its cellular building blocks, namely neurons. In order to understand how the human experience emerges from the neuronal structure of the brain, we must link findings from cellular and cognitive neuroscience. A successful example of this approach can be seen in the multidisciplinary study of hierarchical visual processing. Periodically certain developments in neuroscience research allow us to grasp this problem in a novel way; 'Grandmother cells' provide a link between abstract concepts and single neuron activity (Quiroga et al., 2005), and the demonstration of plasticity at the synaptic level provided a mechanism by which information can be encoded across time. One such advance is the discovery of mirror neurons (MNs) in the premotor cortex of the macaque. This finding and its application to understanding information processing in the human brain will be the focus of this essay.

Mirror neurons respond to the execution of an action, and to the observation of a conspecific carrying out that same action (di Pellegrino et al., 1992; Gallese et al., 1996; Rizzolatti and Craighero, 2004; Rizzolatti et al., 1996a,b).

First identified in the brain of macaque monkeys, these cells have stimulated a wave of research by authors attempting to identify the equivalent cells in the human brain. This section will review critically the evidence for mirror neuron activity in humans and discuss the potential role of mirror neurons in human behavior. This will include a full discussion of the role of mirror neurons in theory of mind (for a more detailed summary of mirror neurons in other aspects of brain function such as language and imitation refer to Rizzolatti and Craighero, 2004).

2. Human mirror activity

2.1. Electrophysiological studies — do humans have a mirror system?

Sensory information received during observation of actions is encoded in terms of a motor echo. This has been demonstrated by electroencephalography (EEG), magnetoencephalography (MEG) and single-cell recordings from human brains. The only study to demonstrate mirror activity at a neuronal level comes in the form of an investigation into nocioception: single cell recordings from the *anterior cingulate* of patients undergoing surgery demonstrate activity in response to both perception and observation of pain (Hutchison et al., 1999). Given that opportunities to carry out such studies are rare, EEG provides a more convenient alternative to invasive techniques.

Normal *mu* wave activity undergoes dysynchronization in response to both action execution and observation (Cohen-Seat et al., 1954; Gastaut and Bert, 1954) as is demonstrated by placing electrodes placed on the scalp. A more sensitive form of EEG has since confirmed these findings; Cochin et al. report that observation and execution of finger movements resulted in reduced power of alpha wave activity (7.5–10.5 Hz) in 20 subjects. They localized this decrease to motor and frontal cortices (Cochin et al., 1998, 1999). Furthermore, Fadiga and colleagues (Fadiga et al., 1995) demonstrated that observation

of actions produced motor evoked potentials (MEPs) in the muscles involved in that movement. This has since been replicated (Strafella and Paus, 2000), and a temporal correlation between the MEPs recorded and the action observed has also been reported (Gangitano et al., 2001). Stimulation of the median nerves during manipulation of an object results in suppression of a post-stimulus rebound effect when recording electrical oscillations from precentral motor cortex (Salmelin and Hari, 1994) using MEG. This post-stimulus rebound event is suppressed to a lesser extent in response to action observation alone (Hari et al., 1998). These results are interpreted as evidence for primary motor cortex activation in response to action execution and observation.

Together these studies provide strong evidence for a human mirror system in the central nervous system which appears to originate from the motor system. The function that this system encodes is the subject of much discussion and will be addressed in later sections. In order to assess further the specific structures of the brain that are involved in this system, a different range of techniques with higher spatial acuity is required.

2.2. Functional MRI and PET studies — where is the human mirror system?

The evidence suggests that the human mirror system stems from activity in the inferior parietal lobe, inferior frontal gyrus (including Broca's area) and superior temporal sulcus (STS) (Rizzolatti and Craighero, 2004). The majority of these studies employ functional magnetic resonance imaging (fMRI). This technology provides information about regional cerebral blood flow in the brain in response to a range of stimuli (blood oxygen level dependent or BOLD effect). From this information it is possible to localize neuronal activity to regions of the brain; however, the neural basis of the BOLD response is far from clear (Logothetis, 2003). Interestingly, the human mirror system appears to overlap considerably with those from non-human primate data; the mirror circuit proposed in the macaque involves projections from the superior temporal sulcus (Jellema et al., 2000; Perrett et al., 1990) to inferior parietal lobe (PF) (Gallese et al., 2002) and ventral premotor cortex (V5) (di Pellegrino et al., 1992; Rizzolatti et al., 1996a,b).

One of the earliest fMRI studies compared action observation, imitation and execution. They found that action execution and observation resulted in activity in left frontal operculum (Broca's area) and right anterior parietal area. Imitation resulted in additional activity in parietal operculum (Iacoboni et al., 1999). The authors report increased activity when the action was imitated which implies that the mirror system may be involved in imitation (see Section 3.1). The protocol used in this study involved a simple finger movement. There is controversy as to the specific stimuli that will target the human system. Mirror activity is only reported in response to object- and goal-related actions and not meaningless intransitive movements in the macaque (Rizzolatti and Craighero, 2004). These data subsequently may not actually reflect what we might call 'mirror activity'. Cortical excitability studies indicate that the MN system is sensitive to all the movements that form an action, not just the action as a whole (Rizzolatti and Craighero, 2004). However, it is not possible to conclude on this in the absence of intracellular

recordings in humans. These properties are distinct from those seen in non-human primates and such differences may explain why humans, but not macaques, have abilities such as theory of mind or advanced imitation.

Grezes et al. (2003) have also compared action observation and execution using fMRI. They found that object-related action observation and execution resulted in increased activation in bilateral dorsal premotor cortex (PMC), intraparietal sulcus, superior temporal sulcus (STS) and right parietal operculum (SII). This study employed the use of an abstract object for the participants to grasp, which, while taking into account the object-related nature of mirror neurons, may not quite fulfil the criteria for goal-related. Furthermore, Gallese et al. (2004) have proposed that the internal object representation may be influenced by one's experience or interaction with it. The use of an abstract 'manipulandum' which has no clear associated action may influence the activity seen in the brain. In addition to this, televized stimuli have been shown to produce a diminished response in the macaque model (Ferrari et al., 2003; Keysers and Perrett, 2004) in certain brain regions, which this study also used. Thus this paradigm may not have targeted putative mirror neurons in an ideal manner. A final and well-structured study investigated the role of context on mirror activity by exposing participants to videos of two types of mug grasping actions (Iacoboni et al., 2005). Unfortunately however, they did not investigate action execution in this study thus few conclusions can be made about mirror activity.

A positron emission tomography (PET) study reported that action recognition was associated with increased activation in the left superior temporal sulcus and caudal inferior frontal gyrus (Rizzolatti et al., 1996a,b). They did not however contrast grasp observation with grasp execution, which is the crucial comparison that would highlight mirror activity. They concluded that human action recognition is represented by a pattern of activity in middle temporal gyrus, STS and left inferior frontal gyrus including Broca's area. However, at no point during their discussion or conclusions do the authors discuss the relevance of their results in terms of human mirror activity. Of interest was the activation seen in Broca's area in response to grasping observation, as this is an area previously thought to be dedicated to language.

A final but important point to note is that the spatial resolution of fMRI, which is higher than that achieved through PET, is in the order of millimetres. As a result it cannot be concluded that an increase in the BOLD response to action execution and observation is conclusive evidence for mirror neurons in the human brain. On the basis of current electrophysiological and imaging data, we are not able to speculate on individual neurons. Accordingly, we are limited to discussing brain areas, as pointed out by Arbib (2005, http://www.interdisciplines.org/mirror/papers/4/2). Whilst it is hard to see why mirror neurons would exist in the macaque brain and not the human brain, ultimately there is no direct evidence of human mirror neurons that respond to action. In summary, there appears to be substantial evidence for a mirror system within the central and peripheral nervous system. However, the evidence attempting to localize this mirror network has some weaknesses; further confirmation and characterization is required. The next question that begs to be addressed is that of function. This comprises the focus of the rest of this essay and is discussed in reference to recognition of intention.

3. How I know why you do what you do

It has been suggested that mirror neurons or the human equivalent may be involved in understanding the intentions of others (Gallese and Goldman, 1998). One can instinctively see how this might occur if components of one's own motor system echo an observed action. In the world of neuropsychology, this ability, unique to humans in its more developed form, is known as theory of mind (ToM).

Theory of mind refers to two concepts: the knowledge that other animals have mental states which may differ from our own; and the ability to infer what these internal states may be. Such states refer to beliefs, goals, intentions or emotions. This term covers a range of skills which may or may not have overlapping neural bases. The term theory of mind fails to distinguish between these two concepts and subsequently tends to imply that possession of a 'theory of mind' or of other minds in itself constitutes the ability to infer the states of other minds. This is doubtfully the case; the knowledge that other people or animals have internal states that differ from our own is more likely a prerequisite for the discrete ability to make correct inferences based on this knowledge. The neuronal mechanisms by which we are able to manipulate this knowledge are also likely to be distinct. In our case, this manipulation may be one of motor simulation as it has been suggested that mirror neurons may be involved in theory of mind (Gallese and Goldman, 1998) and there is accumulating evidence to substantiate this hypothesis.

There are at least three prominent ways in which the role of mirror neurons in ToM processing can be assessed. Firstly it is possible to compare brain areas involved in both ToM and mirror activity. If ToM relied on mirror neuron activity, areas involved in ToM might be expected to display mirror activity. Secondly, studies could be designed to specifically tap into the role of mirror neurons in understanding the intention behind the action. A final approach which would support this theory, would be to look at mirror neuron activity in people with absent or abnormal theory of mind capabilities. The evidence supporting these lines of investigation will be assessed in the following sections.

3.1. Brain areas involved in ToM and mirror function

A network including medial prefrontal cortex (PFC), posterior STS and temporal poles is thought to support theory of mind processes (Frith and Frith, 2003). Investigations which have contributed to these conclusions typically involve carrying out tasks which require inferences to be made, whilst undergoing fMRI or PET scans. Studies which aim to localize function are subject to similar sorts of problems as is the task of localizing mirror neuron activity. These studies will involve different brain processes and regions as they employ a range of experimental approaches. For example, some use written stories (Fletcher et al., 1995; Vogeley et al., 2001) and others use comic strips (Brunet et al., 2000; Gallagher et al., 2000) to target ToM processing. This is an important discrepancy as the involvement and/or requirement of language in ToM is debatable.

Previous work has indicated that temporal language processing areas are involved in ToM (Baron-Cohen et al., 1999; Brunet et al., 2000). Other approaches indicate that language is not *required* for ToM. For example, children with specific language impairments (Perner et al., 1987) and even severe aphasic patients (Varley and Siegal, 2000; Varley et al., 2001) have been reported to have normal ToM processing. This heavily implies that language capacity is not an essential requirement for ToM. Furthermore, language processing areas have also been implicated strongly in mirror neuron studies. Area F5 in the macaque is thought to be the non-human primate analogue of Broca's area (Petrides and Pandya, 1994), an area where a number of studies have reported mirror activity (Grezes et al., 2003; Iacoboni et al., 1999).

Areas implicated in both theory of mind and mirror (Table 1) include superior temporal sulcus (Baron-Cohen et al., 1999) and parts of the frontal gyrus (Fletcher et al., 1995; Iacoboni et al., 2005; Rizzolatti et al., 1996a,b) and temporoparietal junction (Williams et al., 2006). These are extremely rough comparisons and only provide a preliminary comparison to demonstrate that an overlap is a possibility. Given the individual differences in locations of brain structures and landmarks (Amunts et al., 2004), firm conclusions in either direction cannot be drawn from this extremely coarse comparison and further investigation is required. It is important to note that the majority of the studies which have investigated ToM have not differentiated between different types. For instance, inferring the intentions of others may well involve mechanisms which differ from those involved in inferring the beliefs of others.

The most famous test for ToM is one proposed by Dennett (1978): the false belief task is designed to test if one is able to infer the beliefs of others when they are incongruent with ones own beliefs. Whilst this is an elegant way to investigate the question it was designed to answer, it is not ideal for identifying regions of the brain involved in inferring intentions of others, or 'motor theory of mind".

There is a clear distinction between mental simulation of action, actual simulation of action and understanding the intention behind an observed action. There are theories which claim that ToM relies on mental simulation of action (Simulation Theory, see Gallese, 1998); however, this is yet to be confirmed. Nevertheless, the evidence supports a role for the mirror system in the former two of these abilities.

The direct matching theory of imitation asserts that observation of an action produces an internal motor representation in the brain of the observer. The most compelling evidence to date for the influence of mirror neurons in motor memory comes from studies by Stefan et al. (2005). In a previous study, this group demonstrated that motor practice of bidirectional thumb movements influences the direction of subsequent cortically TMS evoked thumb movements (Classen et al., 1998). In other words, if you practice moving the thumb to the left any ensuing evoked movements are more likely to be made to the left. These finding have been replicated in other human (Pascual-Leone et al., 1995) and animal studies (Kleim et al., 1998). More recently, Stephan et al. (2005) have described how the mere observation of thumb movements has the same effect on influencing the direction of subsequent thumb movements. This provides evidence that action observation influences the neural circuits responsible for action execution in a positive rather than inhibitory manner. Given that the mere observation of an action can trigger an internal motor representation of the same action, it is possible to see how mirror neurons may contribute to imitation (Jeannerod, 1994).

Human imaging studies have demonstrated that left inferior frontal and right superior parietal cortices are activated in response to both imitation and observation (Iacoboni et al., 1999). These data provide evidence to support the direct matching hypothesis and indicate that mirror neurons may be involved in the underlying mechanism. Furthermore, PET studies have shown that observation of actions with a view to later imitating the action activates motor areas involved in generation of actions and planning (Decety et al., 1997).

To conclude, according to simulation theory, we mentally mimic actions that we observe allowing us to infer the internal states of others such as their intentions. The evidence for mirror activity in formulating an internal motor representation of an observed action in order to imitate thus corresponds with a simulation theory of ToM. At first glance there appears to be a minor correlation between some of the areas thought to display mirror activity and those involved in theory of mind processing. However, clear characterization of motor ToM and further studies of mirror activity in these brain regions is required before any conclusions can be drawn. A more fruitful

		ToM	MNs
Table 1 – Brain areas involved in theory of mind and those displaying mirror activity			
fMRI		STG amygdala PFC (Baron-Cohen et al., 1999)	Left frontal operculum (Broca's area) Right anterior parietal area (Iacoboni et al., 1999)
		ACC Left temporopolar cortex (Williams et al., 2006)	Posterior inferior frontal gyrus (Iacoboni et al., 2005) Right parietal lobe (Williams et al., 2006) Right anterior parietal cortex (Iacoboni et al., 1999)
PET		Left medial frontal gyrus Posterior cingulate cortex Right posterior STS (Fletcher et al., 1995) (Verbal task)	Left inferior frontal gyrus (BA 45) and left STS (Rizzolatti et al., 1996b)
		Left medial frontal lobe Left temporal lobe (Goel et al., 1995)	Left inferior frontal gyrus (BA 45) and left STS, left parietal lobe, right dorsomedial motor cortex and mesial area 6 (Grafton et al., 1996)
		Right PFC Right ITG Left STS Cerebellum AC MTG (Brunet et al., 2000)	

Functional magnetic resonance imaging and positron emission tomography have been used to investigate which regions of the brain are involved in theory of mind processing. A separate range of authors report areas of the brain which demonstrate mirror activity. Overlap between areas of the brain which are involved in processing both would provide evidence for the role of mirror neurons in theory of mind.

approach may be to target the mirror system and ToM processing within the same experiment.

3.2. Targeting areas involved in understanding action intention

If mirror neurons were involved in inferring intentions from actions, they would be expected to fire in situations when the intention was not known and thus has to be inferred. Umilta et al. (2001) recorded from mirror neurons in macaque F5 and demonstrated that a subset of these mirror neurons fired in response to the action even when the completion of the action was hidden from view. Thus the mirror system appears to be encoding the inference of the intention behind the action. This carefully designed study comprises a paradigm which targets both the mirror system and ToM processing in the same time period. Consequently, this has provided the strongest piece of evidence for the role of mirror neurons in theory of mind so far.

Iacoboni et al. (2005) took the next step and focused in on context within an action in order to elucidate the brain areas involved in inferring an intention. They found that actions within a context specifically result in activity in inferior frontal gyrus and ventral PMC, areas which reportedly demonstrate mirror activity. The authors interpret this as evidence for the role of a subset of mirror neurons in extracting information about action intention from environmental contextual clues.

Together these two studies provide powerful evidence for the role of the human mirror system in understanding the actions of others, both in the macaque and human brain. How this ability differs between the two models remains to be seen. In order to assess the impact this has on understanding the behavior of others it is necessary to look to people who have attenuated theory of mind and/or mirror systems.

3.3. Mirror activity in people with absent or attenuated ToM

Some patients who suffer from abnormal ToM processing also have attenuated mirror responses. Initial studies have focused on the classical condition of abnormal ToM processing: autism. The last few years have seen a cluster of studies indicating abnormal mirror activity is present in autism (Dapretto et al., 2006; Ramachandran, 2001; Williams et al., 2006, 2001). It has been suggested that mu-wave activity may be an indirect measure of mirror neuron activity (Muthukumaraswamy et al., 2004). Oberman et al. (2005) report that the normal mu suppression that is seen during action execution is reduced in people with autistic spectrum disorder. Theoret et al. (2005) report that modulation of activity in primary motor cortex (MI) of patients with autistic spectrum disorder (ASD) is reduced with respect to controls during finger movements. Again however, we must note that these studies have not used object-related goal-directed movement and thus may not reflect the mirror activity. This is not to deny that there may be additional motor abnormalities in these patients.

There may be preliminary structural evidence to support the claim that MNs are involved in autism. A recent article suggested that there is cortical thinning in areas reported to show mirror activity in autism, namely the inferior frontal cortex (IFC), inferior parietal lobe (IPL) and STS (Hadjikhani et al., 2006). These conclusions rely on the previous work outlining the location of the human mirror network being confirmed.

An additional group of people with attenuated or absent ToM processing are healthy children. According to Piaget's theory of development, until the ages between 6 and 11, children are unaware that others have their own mental states that differ from our own (Piaget, 2001). There is some debate as to when ToM appears during normal development. Early studies have indicated that ToM is absent in children below the age of 4 years (Perner et al., 1987; Wimmer and Perner, 1983). Detailed study of children's use of language and more simple tasks where false beliefs are embedded in a play tends to imply that a level of ToM is present as young as 18 months (Frith and Frith, 2003). Thus it would be of interest to investigate how and when MN activity develops during this period and how this may relate to the acquisition of ToM.

A final point: it is not understood how the properties of MNs differ between the human and the macaque. The specific properties of macaque mirror neurons do not appear fully to support their involvement in understanding actions, but macaques are not able to carry out such a task. Examples of these points are highlighted by Csibra (2005). In the macaque model, not all MNs have motor properties (Gallese et al., 1996; Rizzolatti et al., 1996a,b), some MNs respond to more than one type of observed action and that this action may not be the same as the executed action (see Rizzolatti and Craighero, 2004). Thus he stresses MN firing would be misleading if they were solely responsible for interpreting the observed actions of others (http://www.interdisciplines.org/mirror/papers/4). Accordingly, if the human mirror system is involved in ToM, the nature of the system is likely to have advanced or adapted in some way from that of our common ancestor. For example, it is possible that there is an interaction between MNs and other information in the brain which allows humans to make these inferences, such as language or memory. The nature of these changes is not currently understood.

To summarize, data from a variety of fields supports the suggestion that the mirror system may contribute to understanding the behavior of others. In the absence of direct evidence, this hypothesis needs to be addressed from a number of stances. Studies which directly target the mirror system and ToM processing are needed. There are a range of human groups in which the mirror system can and should be investigated. Such exploration would help to illustrate the contribution of the mirror system to mental simulation of action, imitation and ToM. We have yet to characterize fully the mirror system in human ontogenesis and phylogenesis. Such an approach will no doubt provide valuable insights into how the macaque and human brain functions differ.

4. The role of mirror neurons in different types of theory of mind

The specific type of ToM that we have described above is a motor ToM referring to the understanding of the intentions of others' actions. However, ToM is a broad term which covers a range of cognitive abilities, including understanding of intentions, understanding of beliefs and understanding of goals. It is likely

then that these processes have subtly distinct underlying mechanisms. Other forms of ToM include emotional or empathetic processing. A recent study specially compared empathy and inferring action intention (Vollm et al., 2006) and demonstrated that empathy and motor ToM result in overlapping but distinct networks of activity. It reported that medial prefrontal cortex, temporoparietal junction and temporal poles are involved in both processes, but that empathy preferentially recruits emotional processing networks compared with the inference of action intention. It may be that dysfunction of the MN system may be involved in conditions where empathetic processing is distorted such as psychopathy. Evidence from macaque recordings indicates that there are MNs that respond specifically to facial movements (Ferrari et al., 2003). Functional imaging studies have confirmed that the BOLD response to emotional images are different in this group of individuals compared with healthy controls (Deeley et al., 2006; Muller et al., 2003). This hypothetical dysfunction could occur at two levels. If this group are unable to identify visually expressed emotion it might be expected that they would have abnormal MN function. Alternatively, and more likely, the mirror system may function sufficiently to allow correct identification of expression (e.g. "that expression is one of happiness"), but that integration of this information with emotional weight is faulty. In other words, perhaps these individuals can identify expressed emotion but do not feel and therefore empathize with it. Neither of these studies tested whether psychopathic individuals were able to identify the emotion expressed. However, given the aforementioned studies indicating abnormal emotional processing in psychopathy, the latter case is perhaps more likely to be the case. To date no study has investigated the mirror system in this group.

Mirror responses have been reported in both emotional processing and empathy. Imitating and observing emotional facial expressions result in the same response; a reduction in activity in the inferior frontal gyrus (pars opercularis) (Dapretto et al., 2005). Interestingly, this area reportedly shows abnormal mirror activity in children suffering from ASD. Imitating and observing expressions of disgust may also initiate a mirror-like response in the insula (Keysers et al., 2003), and damage to this area can affect both one's emotional experience and assessment of others' emotions (Adolphs et al., 1994; Calder et al., 2000). Showing subjects pictures of painful stimuli and subjecting them to pain results in increased activity in the anterior cingulate cortex (Hutchison et al., 1999). Avenanti et al. (2005) have used transcranial magnetic stimulation (TMS) to reveal that the motor response to experiencing pain (reduction in amplitude of the MEP in the muscle affected) and observing it are similar. The level of reduction in MEP amplitude correlates with sensory empathy measures but not with emotional empathy measures. This may have been because they used a human model which may not elicit a true emotional empathetic response. Singer et al. (2004) demonstrated a partial mirror effect in response to experiencing and/or observing painful stimuli. They demonstrated that knowledge that painful stimuli are being administered to a loved one activates a pattern of activity including anterior insula and anterior cingulate cortex. In contrast to the TMS study these researchers found that the level of activation in these areas correlated with subjective scores of empathy. This study used a different paradigm that led the subject to believe that a loved one was experiencing pain, so that an emotional response may have been more likely. Correspondingly, these data were interpreted as indicating that the awareness of pain in others activates affective aspects of the pain network rather than sensory areas. The involvement of mirror neurons in affect has not yet been investigated and warrants attention.

5. Conclusions

Strong evidence from a range of techniques provides support for the existence of a human mirror system. From the outset, it could be argued that accurate localization of this system in the brain is currently problematic. A variety of paradigms have been used which may target different processes, and few studies have contrasted action execution against action observation in the same conditions that the animal data command. Identification of the human mirror network thus warrants further attention. The evidence suggests that the human body may possess a mirror system, distributed throughout the brain and peripheral nervous system, or a 'motor resonance' (Rizzolatti and Craighero, 2004). This implies the body has a range of mechanisms for mirroring external events that may be involved in understanding the causes and consequences of external events.

There is a substantial amount of evidence to suggest there is some involvement of mirror neurons in theory of mind from all three avenues discussed. The specific role of the cells in ToM remains to be characterized. This may be approached by studying patients with abnormal ToM or during acquisition of ToM in normal development. The types and location of MNs may differ between different types of ToM and this requires investigation.

These studies may demand that a rethink of non-human primate intelligence is required. These recordings imply that macaques have at least the neural circuitry required to interpret the actions of the experimenter in terms of their own motor experience. This is not to say that the animals are able to predict intentions, only that if these cells reflect what we think they might represent in the human brain, then there are implications for ToM and social intelligence in non-human primates.

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