

The social function of the human mirror system: a motor chauvinist view

Antonia Hamilton

Institute of Cognitive Neuroscience, University College London

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Sukhvinder S. Obhi & Emily S. Cross, editors

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Abstract

Many different claims have been made concerning the function and role of the human mirror system. This chapter first examines the question of what makes the mirror system special, and whether this particular network can be clearly distinguished from visuomotor systems in the brain. Current studies suggest it is surprisingly hard to draw clear distinctions between mirroring and visuomotor systems. The second part then distinguishes between models for understanding, predicting and responding to social stimuli. I suggest that responding theories have been somewhat neglected, and that social responding should be considered as an important function of the mirror system, in the same way that grasping objects is an important function of the visuomotor system.

The humble sea squirt provides an excellent example of motor chauvinism – after an early period of active swimming, it settles on a rock and assumes a passive lifestyle of waiting for food to drift by. At this point, it digests its own brain, because a body that does not move has no need for a brain. The motor chauvinist makes the claim that the primary function of the human brain is to move – to decide what actions to perform and then implement those actions in an efficient manner. In this chapter, I examine how this view can help us understand the functioning of the human mirror system.

Mirror neurons were first discovered in the premotor cortex of the macaque monkey in the context of studies of motor physiology (di Pellegrino et al., 1992; Gallese et al., 1996). These neurons respond when a monkey picks up an object, but also when he sees a person pick up an object. However, the macaque monkey's abilities to engage socially and to imitate are somewhat limited. Neuroimaging studies allow us to examine equivalent brain systems in humans to test their role in human social behaviour. A large number of studies have now documented activation of the human premotor cortex and inferior parietal cortex when participants observe actions, perform actions and imitate actions (Caspers et al., 2010; Molenberghs et al., 2012). In this chapter, I focus on the properties of the brain systems that respond when typical adults observe actions – the mirror neuron system (MNS) and consider what role this plays in human behaviour. In particular, I draw comparisons between the MNS and other cortical motor systems for object use (object-motor system - OMS). This comparison aims to highlight which features are similar between the MNS and OMS, and which differ. Then, I consider different theories of the function of the MNS.

What might make the human mirror system special?

Since mirror neurons were first discovered, many claims have been made for the special function of this brain network, that it can provide a unified model of social cognition (Gallese et al., 2004) and transform our understanding of psychology (Ramachandran, 2000). However, before examining the function of the MNS in human behaviour, it is useful to consider if this network has any special properties – is it unique in localisation, or in what categories of stimuli drive its responses, or how it is modulated by experience or by other brain networks? In particular, I address

this question in comparison to cortical motor systems for object use (OMS) which allow people to interact with tools and other objects in everyday life. The aim of this review is to determine if there is anything unique about the MNS which is not true for the rest of the object-motor system.

Cortical localisation

Mirror neurons themselves are not easy to localise in humans, because fMRI operates at a much grosser resolution than single unit recordings. However, multiple studies have tested which brain regions are active when participants observe actions and perform actions. Both at the single subject level (Gazzola and Keysers, 2009) and at the level of meta-analyses (Caspers et al., 2010; Molenberghs et al., 2012), these studies reveal network in the inferior frontal, premotor and inferior parietal cortex (see Box 1). These areas are engaged when participants see hand actions and also when they perform hand actions. Imitation of hand actions (Molenberghs et al., 2009) and imagination of actions (Grèzes and Decety, 2001) engage similar areas. Though it is not possible to record single cell activity within these regions, detailed studies using multivoxel pattern analysis (Oosterhof et al., 2010) and repetition suppression (Kilner et al., 2009) give a clear indication that these regions contain neuronal populations with mirror properties.

Studies of the cortical motor control system have shown that very similar brain areas are engaged when participants perform hand actions without any social context. The basic circuitry for grasping actions includes premotor cortex, supplementary motor area and inferior parietal cortex (Grafton et al., 1996). This frontoparietal network is strongly engaged when participants plan tool use actions (Johnson-Frey et al., 2005), plan familiar gestures (Króliczak and Frey, 2009) and when they imagine actions (Johnson et al., 2002). The critical role of premotor and inferior parietal cortex in performing object directed actions is best illustrated by studies of damage to these regions, which results in apraxia (Buxbaum et al., 2005) and difficulty in tasks requiring planning and executing of hand-object interactions as well as imitation. An influential model of the cortical motor system (Cisek and Kalaska, 2010) suggests that the frontoparietal motor system operates by specifying possible actions in the world (ie. object affordances) and the prefrontal and subcortical regions help in selecting which actions to perform.

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It is particularly useful to compare brain activation when participants observe human actions (i.e. MNS) to activation when participants observe graspable objects or other non-social cues to action. The theory of affordances (Gibson, 1977) suggests that seeing an object leads to an immediate percept of the way that object can be grasped – its affordance. In cognitive terms, this might mean that observing a graspable object automatically engages motor systems for grasping. Several neuroimaging studies suggest that, when participants see graspable objects, they engage premotor and parietal cortices (Grèzes and Decety, 2002; Grèzes et al., 2003). This is also true for tools (Grafton et al., 1997; Kellenbach et al., 2003). Note that photographs of objects or objects which are out of reach do not engage the frontoparietal network in such a robust fashion (Gallivan et al., 2009). These studies suggest that observing objects which afford actions can robustly engage the frontoparietal network in the human brain.

To illustrate more closely the specific regions engaged in different tasks, the table in Box 1 presents an overview of recent literature. Both observation and performance of hand actions

reliably engage SMG, aIPS and PMd. These summary data are taken from recent meta-analyses to ensure robustness (Caspers et al., 2010; Grèzes and Decety, 2001; Molenberghs et al., 2012, 2009). In the case of observation of graspable objects, a formal meta-analysis was not available so the citations represent an informal survey of the available literature. A full meta-analysis of this neglected area would be valuable in future. The data so far indicate that, again, SMG, aIPS, PMd and also IFG are the regions most reliably activated by the observation of graspable objects. Neither performed actions, observed actions nor observed objects engaged PMv or ANG in this summary. The results here highlight that performing actions, observing actions and observing action cues all engage the same regions of the frontoparietal network. The same conclusion is clear in the macaque studies, where mirror neurons are intermingled with canonical neurons and other visuomotor neurons in the same brain areas (Murata et al., 1997; Rizzolatti et al., 1988). Thus, the conclusions here are not novel, but do sometimes seem to be forgotten in the excitement to attribute engagement of the FPN to mirror neurons. Finally, the overlap of motor and mirror systems highlights that cortical localisation cannot be considered as a feature which makes the MNS unique.

Goals and kinematics

What features of the visual world drive the responses of the MNS? It is a requirement that the MNS be tuned to human actions, but several studies suggest this tuning is not tight – the MNS responds equally to human and robotic actions (Cross et al., 2012; Gazzola et al., 2007). Beyond this, it is also possible to distinguish different types of human action. One key debate concerns different levels of representation of action. Any single action can be described at multiple different hierarchical levels. For example, the action depicted in Figure 1 (top) could be described as ‘take the mug’ (goal level) or as a ‘whole-hand grasp’ (kinematic level) or as a set of dynamic muscle movements. Both goal-level and kinematic-level representations of actions are present in the MNS, with some debate concerning their precise localisations. A series of studies using repetition suppression methods suggest that left aIPS represents the goal of an action (Hamilton and Grafton, 2006; Ramsey and Hamilton, 2010) while IFG represents actions at a kinematic level (Hamilton and Grafton, 2007; Kilner et al., 2009). In other studies, parietal cortex is sensitive to the relationship between hand and object (pull v. push) while premotor cortex is sensitive to the effector used (Jastorff et al., 2010).

The same distinction can be found in studies of visuomotor control. Performed actions which differ in terms of kinematic features can be distinguished in inferior frontal cortex (Kilner et al., 2009), while actions which differ in terms of object-goal can be differentiated in aIPS (Oosterhof et al., 2012). Both premotor cortex and aIPS show repetition suppression when participants perform the same tool use action twice in a row (Valyear et al., 2012), but not when they perform arbitrary actions with the same tools. Grasping the same object twice in a row leads to adaptation in aIPS and left SMG (Króliczak et al., 2008), indicating that these regions are sensitive to object identity as well as the kinematic parameters of grasping. In another study, both premotor cortex (PMv and PMd) and aIPS are selective to different types of performed grasp (Fabbri et al., 2014).

Overall, these studies suggest that both the MNS and the OMS are tuned to similar dimensions of action. For both observed actions and observed objects, studies can distinguish goal-

related action representations (e.g. those sensitive to object identity) and also kinematic action representations. There are hints in both datasets that the parietal components of the frontoparietal network have a stronger role in encoding action goals, while the premotor regions are more relevant for action kinematics. However, it is likely that there is overlap in this classification for both social and non-social cues.

Behavioural response priming

Automatic imitation is a behavioural effect which arises when participants view an action and are instructed to perform another action, which could be congruent or incongruent (Brass et al., 2001). Responses are faster for congruent actions, and this robust behavioural effect can be taken as a measure of the link between a performed and observed action (Heyes, 2011). Similar priming effects can be observed for other visuomotor phenomena, such as object affordances. For example, responses to an image of a tool are faster when the responding hand is on the same side as the graspable part of the tool (Tucker and Ellis, 2004) and this effect depends upon the FPN (Grezes et al., 2003). Recent work shows the effect is stronger for grasps related to the object's function, showing that even basic priming can be influenced by action goals (Masson et al., 2011). Together, these studies suggest that similar processes govern priming of imitative responses and priming of responses to objects.

Familiarity & training

Many studies have shown that familiarity with actions is a key factor influencing responses in the MNS. BOLD signals during action observation are larger when participants view actions they are familiar with and can perform themselves, compared to novel actions (Calvo-Merino et al., 2005). Familiarity is also a key driver of activation in the OMS. Responses to familiar tools and stimuli which are linked to motor responses are much stronger than to unfamiliar or novel objects (Valyear et al., 2012). These studies all suggest that viewing familiar stimuli which are linking to motor responses, either action stimuli or object stimuli, can robustly drive engagement of the MNS or OMS.

However, contrary to these results, there are also cases where unfamiliar actions elicit a greater BOLD signal in the MNS. Viewing unfamiliar, robotic dancing leads to more engagement than viewing familiar, smooth dancing (Cross et al., 2012). Planning novel actions can also lead to greater BOLD activation than planning familiar actions (van Elk et al., 2012). Explaining these different patterns of activation is not entirely straightforward – in some context, increases in familiarity may lead to increased neural recruitment, but in other cases learning may lead to more efficient encoding and less recruitment (Wiestler and Diedrichsen, 2013). One solution to this difficulty is to use MVPA approaches which reveal a clearer distinction between different motor patterns after learning (Wiestler and Diedrichsen, 2013) but this has not yet been applied to observed actions.

Another approach to understanding the role of stimulus familiarity in driving responses in the MNS or OMS is to train participants to make new stimulus-response associations, thus achieving complete control of the level of familiarity with experimental and control stimuli. In an early study, Cross et al showed increases in MNS activity when participants viewed learnt dance sequences compared to matched novel sequences (Cross et al., 2006). Using training, it is also possible to

induce responses which run counter to the common mirror neuron principle that observed and performed actions should match. If participants learn to make a hand action every time they see a foot action, and to make a foot action every time they see a hand action, then BOLD signal when viewing hand actions is strongest in 'foot' related parts of premotor cortex, while BOLD signal when viewing foot actions is strongest in 'hand' related parts of premotor cortex (Catmur et al., 2008).

Training is also critically important in the responsiveness of cortical motor systems to objects. In a detailed study, Creem-Regehr and colleagues trained participants to use novel objects as tools in different ways. Observation of the trained tools during fMRI led to engagement of bilateral IPL and IFG, while observation of novel objects which had not been trained as tools did not (Creem-Regehr et al., 2007). Different types of training differentially affect activation of the OMS. If participants are trained to manipulate novel objects, they later activate left IFG and left IPL when viewing the objects, but this pattern is not seen for objects which are trained in a purely visual manner (Bellebaum et al., 2013). These results emphasise that activation of the FPN when viewing objects is driven by links between the objects and possible actions.

Training methods have also been used to directly test whether the MNS behaves in the same way as the OMS. Data suggest that if participants are trained to respond to arbitrary visual cues (coloured circles) with finger movements, then viewing these cues leads to engagement of the same regions (aIPS and premotor cortex) as observing or performing the actions (Landmann et al., 2011). Another study directly contrasted arbitrary cues and observed action cues (Cross et al., 2009). Participants were trained over the course of a week to perform novel dance sequences in response to arrow cues in a video game. During fMRI scanning, they observed sequences of arrow cues associated with both trained dances and untrained dances, and each of these could include a human dancer behind the arrows or not. This gives a 2x2 factorial design crossing the factors *training* and *human action observation*. The results show that PMv was more robustly activated when participants viewed trained sequences compared to untrained, but was not sensitive to the presence or absence of a human dancer. The converse pattern was seen in superior temporal sulcus, with greater activation when viewing sequences with a human dancer regardless of training status. This suggests that engagement of PMv is driven by motoric familiarity with a particular sequence, and not by the requirement to observe or understand another person.

A stronger test of similarity between the MNS and OMS is to use methods that give a more detailed measure of sensorimotor links. For example, one of the best demonstrations of mirror neuron responses in the human MNS used a cross-modal repetition suppression method (Kilner et al., 2009). In this approach, participants execute an action (e.g. ring-pull) and in the next trial see an action (e.g. twist OR ring-pull). In cases where the performed action matches the observed action, repetition suppression means that a smaller BOLD signal should be expected from mirror neurons (but not from visual-only or motor-only neurons). Such a pattern was found in inferior frontal gyrus. Recently, Press and colleagues trained participants to make new sensori-motor associations (e.g. see purple square → do thumbs-up sign) and then used a repetition suppression approach to search for brain regions showing crossmodal visual-motor links. For example, if participants had been trained to link a purple square to a thumb action, and then performed a thumb action in the scanner followed by viewing a purple square, one would predict a suppressed response to the visual stimulus as part of a trained link. In contrast, if a performed thumb action was followed by an untrained stimulus (orange circle), no suppression would be expected. The predicted pattern of BOLD was

found in both PMv and IPL. These results suggest that both visual action-motor links and visual cue-motor links can be found in similar brain regions with similar methods, and that the latter can be induced with simple training procedures.

Overall, these studies of training and familiarity suggest that both the MNS and OMS are strongly engaged by observing stimuli which are linked to motor responses. Furthermore, patterns of BOLD response following training are very similar for familiar observed actions and trained symbolic cues. The implication of such studies is that the same associative, sensori-motor processes underlie both response to observed actions and responses to other visual cues. Detailed discussion of what this means for our understanding of the origins of the MNS can be found elsewhere (Cook et al., 2014).

Summary

The data reviewed so far aimed to summarise the properties of the human mirror system, and to determine if any of these are unique and unlike other sensorimotor systems. These studies suggest that the MNS and OMS are located in the same cortical regions. Both are sensitive to action goal and action kinematics, with a preference for goals in parietal regions. Responses to both observed actions and observed objects are substantially modulated by familiarity. Training seems to be able to generate new sensorimotor links which are indistinguishable from the links between performed and observed actions. This means that the only 'special' feature of the MNS which distinguishes it from the OMS is that the MNS responds to observed human actions while the OMS responds to objects. Is this distinction enough to attribute very different cognitive and functional properties to the MNS? The remainder of the present chapter instead focuses on theories of MNS function, and considers how our knowledge of the MNS and OMS can inform these theories.

What is the function of the MNS?

While many different theories of MNS function have been proposed, here I distinguish between three major types of theory, as illustrated in Figure 1. All three consider the same four basic components – visual inputs, visual representations of actions, motor representations of actions and motor outputs. More subtle distinctions between goal and kinematic representations or other categories are found in these models, but the present summary glosses over these for simplicity. The models differ primarily in how the four basic components are connected and process information. To introduce each, I provide a little historical background.

When mirror neurons were first discovered in the premotor cortex of the macaque monkey (di Pellegrino et al., 1992; Gallese et al., 1996), it was important to distinguish 'motor' activation of these neurons from perceptual activation. A key aim of these early studies was to demonstrate that these patterns of neural activation were not 'just' sub threshold motor activation, as the monkey prepared to perform an action, but rather reflected some level of understanding of the observed action. Thus, early studies showed that the monkey did not move its own hands at the time of mirror neuron activation, and emphasised explanations in terms of recognising or understanding the observed actions.

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Similar to the macaque studies, early studies of the human MNS focused on explaining MNS activation in terms of understanding actions (Buccino et al., 2001) and aimed to rule out motor involvement (Rizzolatti and Craighero, 2004). Research focused on the contribution of the human MNS to imitating actions (Buccino et al., 2004b; Iacoboni et al., 1999) and understanding action goals. Similarly, theories of MNS function emphasised the novel idea that basic motor systems could make an important contribution to cognitive and even perceptual functions within the social domain. Important data here showed how the MNS is active when people observe meaningful (Buccino et al., 2004a) and familiar (Calvo-Merino et al., 2005) actions, and is essential for judging action kinematics (Pobric and Hamilton, 2006). From these studies, the theory that mirror neurons are for *action understanding* was developed. This model places an emphasis on the idea that motor representations allow an observer to feel an action 'from the inside' (Rizzolatti and Sinigaglia, 2010) and are important in understanding why other people perform actions (Figure 1A). Thus, motor systems could make a contribution to social and cognitive processes. This was a very novel idea and generated substantial research. However, it was also debated whether the MNS alone could provide action understanding or whether other cognitive processes were needed (Csibra, 2007; Jacob and Jeannerod, 2005).

In considering how actions might be understood, researchers realised that for an individual observer, reflecting on why an action was performed after it is complete (retrodicting) is often less useful than *predicting* what action will be performed next. ERP data demonstrate that premotor cortical regions are activated in anticipation of a future action (Kilner et al., 2004; Southgate et al., 2009) and eye gaze while observing actions is also predictive (Flanagan and Johansson, 2003). Building on these ideas, the *predictive* theory of the mirror neuron system emerged (Kilner et al., 2007; Wilson and Knoblich, 2005). Under this model, the primary purpose of the MNS is to predict what actions another person will perform, drawing strongly on top-down processes. For example, contextual information and prior knowledge can be used to generate a set of possible actions a person might perform and then to make more detailed predictions about the visual input should those actions occur. The predicted visual patterns can then be compared to the incoming visual information to determine what action was actually performed (Figure 1B). This model fits within a broader Bayesian predictive framework (Friston et al., 2011) which attempts to explain the function of the brain in terms of a need to minimise prediction error in visual and motor systems. Bayesian predictive models are fairly well established in sensory systems, but it is not yet clear if they provide a useful account of motor systems.

The new social prediction account

Both the action understanding and action prediction accounts of the MNS are problematic in two ways. First, they largely ignore the parallels between the MNS and OMS highlighted above, and thus do not take into account what models of motor control might be able to tell us. If the MNS and OMS are entirely intertwined and seem to operate on similar principles, it would be odd to suggest that the primary function of the MNS (understanding/prediction) is entirely unrelated to the OMS. Second, it is clear that both the predictive and understanding frameworks are largely concerned with passive observation. If you watch a familiar movie, you might be able to predict what will happen in every scene, but you still cannot be part of the action. In real-life situations, it is critical to respond to others in a timely fashion, and to dynamically interact (Pfeiffer et al., 2013a). Such dynamic interaction is rarely studied in the lab because it is hard to control and experimentally manipulate.

New methods such as virtual reality (Pfeiffer et al., 2013b; Zanon et al., 2014) are gradually reducing this problem. This approach is sometimes termed ‘second person neuroscience’ (Schilbach et al., 2013), and it suggests that when using realistic and interactive tasks, we may engage more and/or different cognitive and neural resources, compared to traditional passive observation studies.

Here I present a social responding account of the MNS (Figure 1C), which builds on previous work (Dezecache et al., 2013; Hamilton, 2013; Schilbach et al., 2013; Wang and Hamilton, 2012), and sets out in more detail how considering social responses can help us understand the function of the MNS. Key to this discussion is the idea that situations can contain *social affordances*, that is, “possibilities for interaction provided by others” (Schilbach et al., 2013). An object may have a particular motor affordance (a pencil affords drawing), and similarly a social situation may have a particular social affordance (an outstretched hand affords a hand-shake response). There is evidence that being in a joint action context can change the perceived affordances of objects (Richardson et al., 2007). However, social affordances can go beyond this and comprise a purely social response to another – seeing a smiling face might afford a smile in return. In this context, the role of the MNS is not just to observe and understand the situation, but rather is to produce the appropriate motor response. A similar position has been set out from a philosophical point of view (Brincker, 2011), suggesting that the MNS and OMS together represent an affordance space of the possible social and non-social actions available to allow action planning.

Building on the idea of social affordances, I suggest that the implementation and use of social affordance in the MNS directly parallels the implementation and use of object affordances in the OMS (Cisek and Kalaska, 2010). Following Cisek & Kalska’s motor model, it seems likely that the parietal cortex can specify the possible social responses afforded by the other people in the current environment, passing this information forward to premotor cortex. Evaluative processing in prefrontal cortex and subcortical areas can then select which of the plausible motor responses should actually be implemented. This scheme can work for social stimuli (MNS) in just the same way as it works for non-social stimuli (objects), with response specification and selection in each case being strongly influenced by past experience and associative learning. The primary difference between social and non-social affordances is that social stimuli are more dynamic and likely to change faster than objects.

There are several lines of evidence hinting that social responding is important in determining the behaviour of the MNS, though this idea has not yet been tested directly. In a study of automatic imitation, Liepelt and colleagues asked participants to respond with a left or right hand action to an image of a left or right hand performing a grasping action (Liepelt et al., 2010). In these trials, participants respond faster to a left hand image with a right hand action, because the visual stimulus provides a mirror image of the response hand, similar to the effect typically found in automatic imitation studies (Heyes, 2011). However, when participants see an image of a left or right hand outstretched to shake hands with the participant, they respond faster with the complementary hand (left hand to left image, right hand to right image). This reflects the socially learnt way to shake hands, rather than being a mirror image of the visual stimulus. Thus, response priming effects reflect social affordances rather than just mirroring.

Another study measured the excitability of primary motor cortex during observation of actions using TMS (Sartori et al., 2013). This is commonly considered a measure of mirror neuron

system activation (Fadiga et al., 1995). In this case, participants observed a video of an actor grasping a coffee thermos with a whole-hand grasp, and the participant showed motor facilitation consistent with performing a whole hand grasp, as an action understanding account of the MNS would suggest. However, the video stimulus then showed the actor reaching towards the viewer to pour coffee into a small cup. The socially appropriate response at this point would be for the viewer (the participant) to pick up the small cup and move it toward the actor. At this point, the motor facilitation seen in the participant switched to that appropriate for grasping a small cup, that is, for the appropriate motor response. This key study suggests that the MNS can engage in understanding actions when a participant is in a passive context, but switches to active responding when that option becomes useful.

A different approach is to examine the timing of social responding. Conty et al showed participants images of neutral or angry actors pointing or gaze at or away from the participant (Conty et al., 2012). Using ERP and fMRI, they report that seeing an angry person pointing towards the participant lead to a robust premotor effect only 210 msec after stimulus onset. This early response to emotion and gesture would not be predicted in a purely action understanding account because anger is not normally imitated (Bourgeois and Hess, 2008). However, it makes sense if the premotor activation reflects response preparation – an anger gesture towards the participant is a potent cue to do something, and premotor cortex is a good candidate for activation of possible social responses.

It is also worth considering the brain systems linked to social affordances. In reviewing the study of anger perception described above, (Dezecache et al., 2013) point out that this social responding requires brain systems both within and beyond the MNS. Specifically, amygdala is critical to the detection of the emotional facial expression in the stimuli. Other studies also suggest that social responding draws on more than just the MNS. Wang et al have shown that eye gaze rapidly enhances the automatic imitation of hand actions (Wang and Hamilton, 2013; Wang et al., 2011a) and that this effect is implemented by a top-down control system in medial prefrontal cortex (Wang et al., 2011b). The idea that control signals from outside the frontoparietal network influence action selection in that network closely parallels the object-motor control model from (Cisek and Kalaska, 2010) in which object affordances in the frontoparietal network are subject to control and selection processes from prefrontal cortex and subcortical regions.

To summarise, the social responding theory of MNS function is a relatively new approach which makes testable claims: that the MNS is engaged by the possible actions which a participant can perform in response to a social stimulus (social affordances); that other cortical regions work with the MNS to select and implement these actions; that the MNS is most strongly driven by familiar stimuli for which robust likely motor responses exist. This model implies close parallels between the MNS and object-motor system, with both having very similar selectivity, cortical localisation and functioning. The review of object-motor systems and mirror neuron systems in the first half of this chapter provides evidence for these claims.

The social responding model goes beyond our traditional, passive approach to social cognition where participant in a lab observe stimuli. In this context, understanding or predicting the visual information might be appropriate. But in the real world, understanding or prediction of actions is a secondary function to the more important requirement to respond appropriately to

others. This means that the social responding theory of the MNS is a motor chauvinist theory, which focuses on the need to perform a motor response. If like the mature sea squirt, people just watched the world drift by, we might not need a motor system (or a brain). As active, engaged interactors in the world, we need both a mirror system and motor system together to find, plan and execute the social and non-social actions that change our world.

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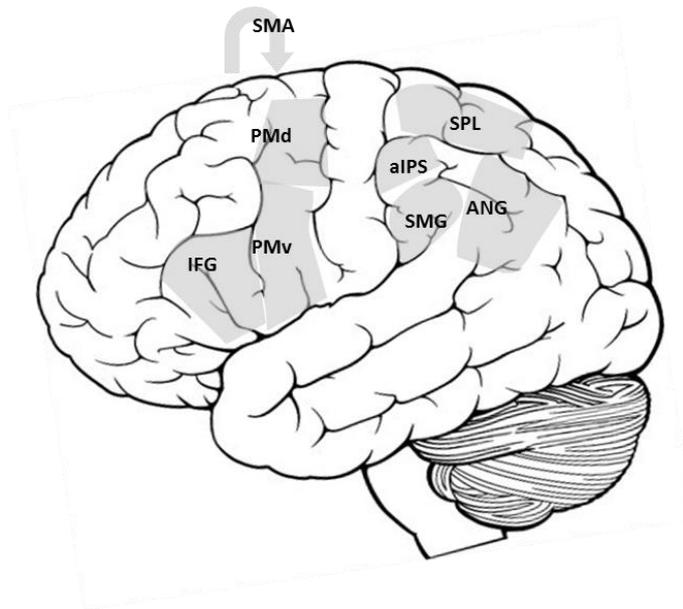
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Box 1

A



B

	Left Hemisphere								Right Hemisphere							
	ANG	SMG	aIPS	PMd	PMv	IFG	SPL	SMA	ANG	SMG	aIPS	PMd	PMv	IFG	SPL	SMA
Observe hand actions		B G	B	B		B	B G	B		B G	B	B		B	B G	B
Perform hand actions		F L	L	F L			F			F L	L	F L			F	
Observe graspable objects		G D C	K D A	H A		G K C		G		H D C	D	H		C		
Imitate hand actions		B I	B	B I	B	B	I	B		B I		B I	B	B	I	B
perform/observe overlap		J E	E	E	E	J	J E			J E	J E	E		J		

Box 1. A. Sketch of brain regions involved in visuomotor tasks. IFG inferior frontal gyrus; PMv ventral premotor cortex; PMd dorsal premotor cortex; aIPS anterior intraparietal sulcus; SMG supramarginal gyrus; ANG angular gyrus; SPL superior parietal lobe; SMA supplementary motor area.

B. Table shows the involvement of these regions in different tasks. Letters show which paper provides this evidence, from the following list. Note that meta-analyses have been cited where possible. **A** Buxbaum, Kyle, Tang & Detre, (2006) Brain Research; **B** Caspers, Zilles, Laird, & Eickhoff (2010) NeuroImage; **C** Creem-Regehr et al (2007) Journal of the International Neuropsychological Society; **D** Gallivan, Cavina-Pratesi, & Culham (2009) The Journal of Neuroscience; **E** Gazzola & Keysers (2009) Cerebral Cortex; **F** Grèzes & Decety (2002) Neuropsychologia; **G** Grèzes & Decety (2001) Human Brain Mapping; **H** Handy et al (2003) Nature Neuroscience; **I** Molenberghs, Cunnington & Mattingley (2009) Neuroscience and Biobehavioral Reviews; **J** Molenberghs, Cunnington & Mattingley (2012) Neuroscience and Biobehavioral Reviews; **K** Valyear et al (2007) NeuroImage; **L** Van Overwalle & Baetens (2009) NeuroImage

Figure 1

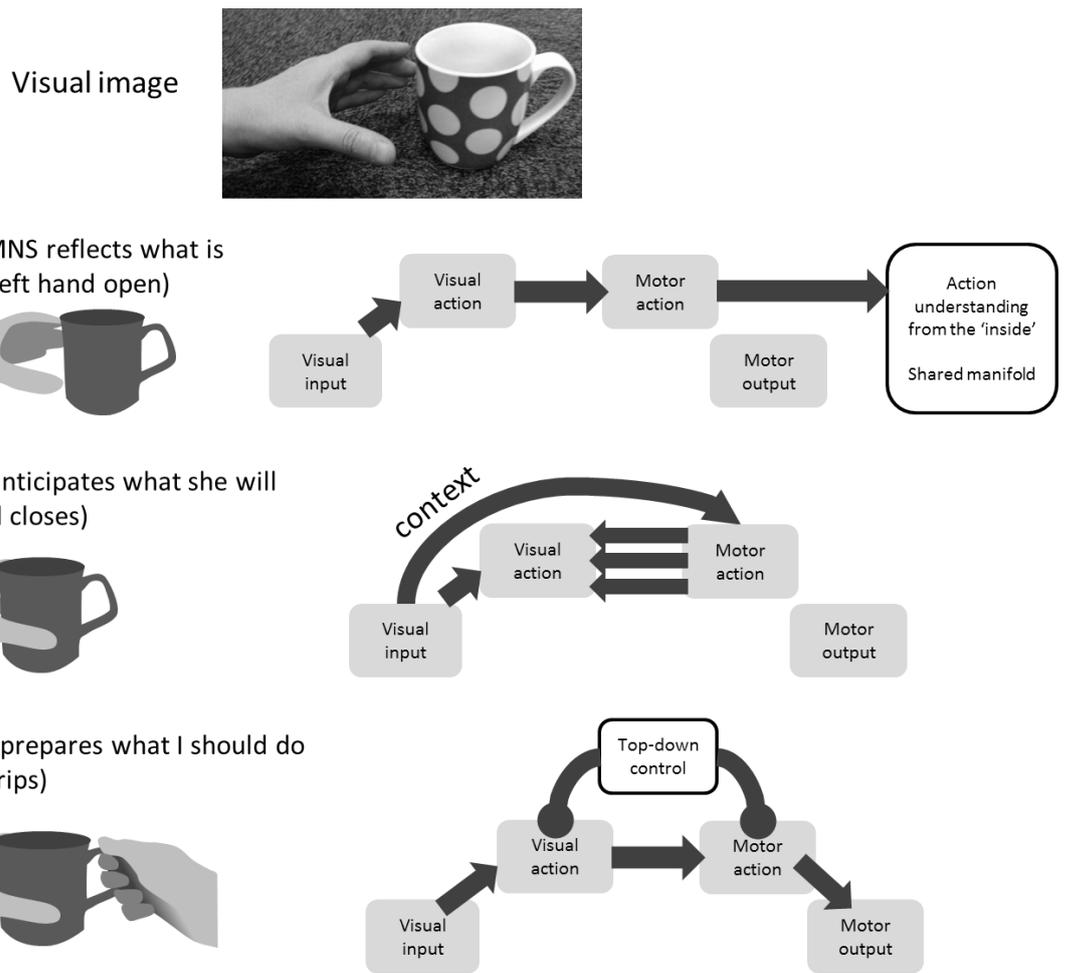


Figure 2. Theories of MNS function. **A. Understanding theories** suggest that the MNS provides a motor representation of what the other person is doing which can be used to understand the action ‘from the inside’. **B Prediction theories** emphasise the role of top-down signals in predicting what action another will perform next. **C. Responding theories** connect the MNS to motor outputs and suggest that the primary role of the MNS is to produce socially appropriate responses.