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Discussion forum

The mirror neuron system contributes to social responding

Antonia F. de C. Hamilton

School of Psychology, University of Nottingham, London, UK

Observing other people in action reliably activates a network of regions across the human premotor, inferior parietal and middle temporal cortex (Caspers, Zilles, Laird, & Eickhoff, 2010). The frontal and parietal components of this network are widely believed to contain mirror neurons (Rizzolatti & Sinigaglia, 2010). The function of the human mirror neuron system (MNS) has been much debated, with a focus on the comprehension (Rizzolatti & Sinigaglia, 2010) and prediction (Kilner, 2011; Wilson & Knoblich, 2005) of other people's actions. This interpretation assumes that the participant is primarily a passive observer (as is often the case during fMRI) and ignores two key factors. First, in real life people do not just observe but rather respond and engage in social interactions. Second, the MNS is embedded within and intimately linked to the motor system. Here, I suggest that an important purpose of the MNS is not to understand or even to predict, but rather to respond, in real-time and in a socially appropriate fashion, to the actions of others (see Fig. 1). This paper reviews three important studies which point to this interpretation.

Behavioural evidence for a human MNS is largely derived from studies of automatic imitation (Heyes, 2011). A study in this tradition asked participants to use their left or right hand to form a particular shape (shake-hands/fist/grasp) in response to images of a left or right hand in the same posture (Liepelt, Prinz, & Brass, 2010). When viewing a right-handed fist or grasp, participants made faster responses with their left hand (a mirror image of the stimulus hand) in line with previous results and with the hypothesis of a predictive-MNS. However, when viewing a right-handed shake-hands image participants responded faster with their own right hand, which does not mirror the stimulus and thus is not a predictive response. Rather, this effect is driven by the strongly learnt social response to seeing a handshake offered and responding with the non-mirror hand. This novel result suggests that compatibility effects in automatic imitation can be driven by social response preparation. The finding that faster responses for complementary actions can be seen in certain contexts (van Schie, van Waterschoot, & Bekkering, 2008) also supports the idea that these paradigms tap more than basic mirroring. Many other studies also show strong MNS responses to learnt social cues (Catmur, Walsh, & Heyes, 2007; Heyes, 2011), but do not distinguish if it is the *learning* or the *social* is more important. If a major purpose of the MNS is predicting other people's responses, it would make sense for this system to be tuned specifically to biological motion or human forms (Press, 2011). One recent study directly tested this (Cross, Hamilton, Kraemer, Kelley, & Grafton, 2009). Participants were trained to make foot movements to arrow cues in a dance video game and then were scanned with fMRI while passively watching the stimulus videos. These videos fell into a 2×2 factorial design contrasting human form (arrows alone or arrows superimposed over a dancing human) and training (learnt or novel videos). The analysis showed that premotor cortex responded selectively to the trained cue sequence but did not respond to the presence of a dancing human. This is hard to explain under the hypothesis that predicting human actions is important in the MNS. However the results are compatible with the claim that the MNS is engaged by familiar stimuli that are associated with learnt responses (see also Press et al., 2012). Thus the results favour a social responding account of the MNS over the human action-prediction account.

Finally, a recent TMS study provides exquisite evidence that MNS engagement is driven by social reciprocity (Sartori, Bucchioni, & Castiello, 2012). Participants watched videos of action sequences while motor evoked potentials (MEP) were recorded from hand and finger muscles. The videos showed an actor pouring coffee (whole hand grip) or sugar (precision grip) into a set of cups. At the start of the videos, participants showed a large MEP when observing a whole hand grip and a small MEP when observing a precision grip, consistent with the mirroring hypothesis. The key manipulation came

E-mail address: a.hamilton@ucl.ac.uk.
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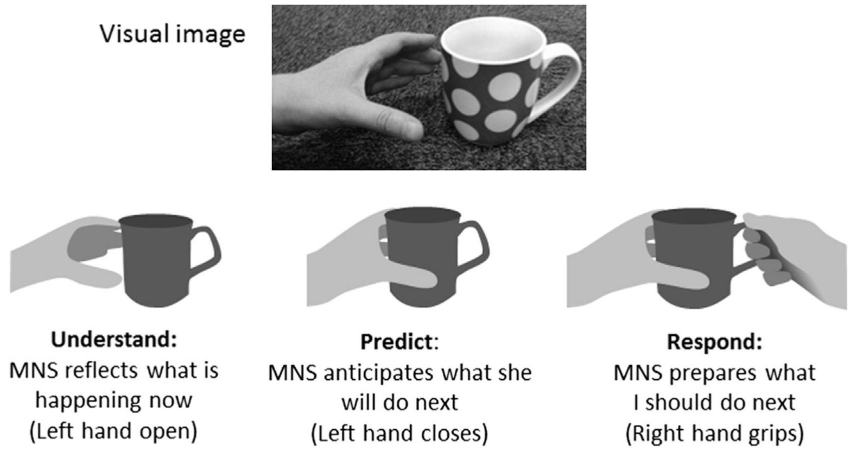

Fig. 1 – Three possible functions of the MNS. Understanding and prediction both involve representing the action of the other person (hand of the left) but responding involves representing one's own action (hand on the right). The papers reviewed here support the idea that the MNS has a key role in social responding.

towards the end of each video, when the actor stretched towards the last cup which was placed close to the participant. The socially appropriate response, if this was a live interaction, would be to pick up the cup and offer it to the actor. At this point, the MEP sizes also changed, with a large response when the cup-to-move was large, and a small response when the cup-to-move was small, even though the actor in the video maintained the same grip and the participant did not perform any actual response. This is not compatible with a predictive-MNS hypothesis, which requires that MEPs should remain tied to the grasp of the observed actor. However, it is compatible with the social responding hypothesis because the MEP size matches the socially appropriate response which could be performed by the participant.

These three studies use different methods and tasks to provide powerful hints that an important role of the human MNS is to specify and implement appropriate responses to social cues. This flexibility goes beyond just mirroring the actions observed (see also Newman-Norlund, van Schie, van Zuijlen, & Bekkering, 2007). There are clear parallels between this model of the MNS and current models of human motor control (Cisek & Kalaska, 2010). In motor control, parietal & premotor cortex specify the different potential actions available in the environment (e.g., a mug is graspable), while frontal and subcortical brain systems have a critical role in selecting which of the possible actions to implement. An equivalent model can be considered for the MNS (Wang & Hamilton, 2012), where parietal and premotor mirror systems specify possible social responses based on previous learning, and frontal and subcortical biasing signals determine which are implemented (Wang, Ramsey, & Hamilton, 2011). This leads to a number of critical further questions: do mechanisms for social responding differ from non-social responding? How does action-prediction relate to social responding? Which of these dominates in the human MNS? How does the MNS relate to other perceptomotor systems in the human brain? Further studies using ecologically valid paradigms may be able to shed more light on how the MNS contributes to interacting with and responding to other people in the real world.

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