

Editorial: Cortex Discussion Forum on “The meaning of mirror neurons”

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The contributions to this Discussion Forum have emerged from and around a Debate that was held in October 2012 at the University of Glasgow (UK). The topic of the Debate was related to the potential “meaning” of mirror mechanisms for human social cognition and behaviour rather than to methodological issues of measuring mirror neurons or to debates about their existence in humans.

To behave socially, humans need to be able to understand and predict others' actions and intentions, which is now understood to be largely an “embodied” process in that humans intuitively match their own body “knowledge” with the perception of others in order to achieve aligned representations (e.g., [Gallese and Sinigaglia, 2011](#), [Kessler and Miellet, 2013](#), [Kilner et al., 2004](#) and [Meltzoff and Moore, 1997](#)). Accordingly, implicit body resonance and alignment with others is not only frequently observed during social interaction in form of subconscious mimicry and so-called “chameleon effects” (e.g., [van Baaren et al., 2009](#) and [Chartrand and Bargh, 1999](#)), but has also been demonstrated to have direct effects on social judgements and pro-social behaviour (for review see [Niedenthal, Barsalou, Winkielman, Krauth-Gruber, & Ric, 2005](#)).

It is therefore crucial for our understanding of human social behaviour to investigate how the human brain solves the ‘correspondence problem’ ([Brass & Heyes, 2005](#)) of mapping visual representations of observed actions onto the observer's own motor system. This is clearly not a trivial task, but it is now widely accepted that mirror mechanisms play a key role, even if the nature of these mechanisms is heavily debated – as reflected in the current collection of papers.

The wider focus of this Forum on the possible consequences of a mirroring capacity in humans and other species further explains the wide variety of notions proposed across the contributions. We will briefly summarize each paper in the following sections and propose a few overarching views and conclusions in the final section of the Editorial. We would like to sincerely thank all contributors for their efforts, especially the Debate Panel [Natalie Sebanz, Harold Bekkering, Geoff Bird, and Vittorio Gallese (via Skype)] and their excellent moderator Dave Perrett. (Videos of the Debate can be viewed and downloaded at: <http://www.psy.gla.ac.uk/events/index.php?id=1599>.)

1. Overview of contributions in this Special Issue

(1) Mirroring in monkeys and apes

Some have argued that mirror neurons may play an important role in imitation and social learning. However, they were originally observed in macaques who show little evidence of imitation in general. [Whiten \(2013\)](#) revisits this argument highlighting recent evidence for social learning and imitation in monkeys and apes ([Whiten, 2012](#)). He goes on to speculate that the more limited imitation (and its lack of precision) in these animals may reflect a much higher proportion of broadly congruent than strictly congruent mirror neurons in apes or monkeys than in humans.

(2) Mirroring attributed to generic learning and cognitive inference mechanisms rather than genetically coded neurons

[Cook and Bird \(2013\)](#) call for healthy skepticism as to two central assumptions about the nature of mirror neurons. First they ask whether they really mirror and second whether they really code for action goals. They suggest that a careful look at the field properties and putative functions of mirror neurons shows that their performance and function is much more diverse and complex than is often suggested in the ‘headline’ reviews about them.

[Heyes \(2013\)](#) also takes a somewhat skeptical position about the special nature of mirror neurons (see [Cook, Bird, Catmur, Press & Heyes, 2013](#)). Specifically she argues that 1) mirror neurons do not consistently encode action ‘goals’, 2) the contingency- and context-sensitive nature of associative learning explains the full range of mirror

neuron properties, 3) human infants receive enough sensorimotor experience to support associative learning of mirror neurons, and 4) mirror neurons can be changed in radical ways by sensorimotor training.

[Wilson \(2013\)](#) also considers the emergence of mirror neurons as part of a more general neural development in which the brain maps between stimuli across very different domains. While this notion is compatible in principle with the associative learning hypothesis (Heyes), Wilson crucially points out that humans are not unbiased “associators”, since our bodies are uniquely isomorphic to those of others, thus, imposing essential constraints on what visual input can be most easily mapped onto what effector output. She raises the intriguing possibility that mirror neurons represent a kind of perceptual-action synaesthesia not so different from the less common synaesthesias relating pitch to height or numbers to colours, by referring to the more general cognitive principle, where isomorphism is exploited (sometimes unwillingly, such as in synaesthesia) for establishing novel associations between distinct representations.

Taking a more cognitive stance [Barsalou \(2013\)](#) argues that the phenomena of ‘social mirroring’ is not mediated by the firing of mirror neurons but reflects a general pattern completion inference process ([Barsalou, 2009](#)). As we experience the world we build up integrated conceptualizations of the whole experienced situation. Subsequent cuing of any component of the situation will activate aspects of the situation as a whole including mirroring. In this way social mirroring is just one of many responses arising from more general learning and inference processes.

(3) Mirror neurons and social responding; extending the simple account

Going back to the origin of the mirror neuron debate [Gallese \(2013\)](#) argues that mirror mechanisms play a central role in what he calls Embodied Simulation (ES). He argues that ES underpins our non-propositional, non-meta-cognitive understanding of inter-subjective relations ([Gallese & Sinigaglia, 2011](#)). In particular, he argues that mirror mechanisms enable us to establish second person I-you relations with those we interact with and that this provides a different embodied understanding than the standard third person perspective.

[Hamilton \(2013\)](#) discusses three functions that have been proposed for mirror neurons: action understanding, action prediction and preparing socially appropriate responses to actions. On the basis of recent human mirror system experiments she argues strongly for the last of these thereby emphasizing the complementarity of responses often associated with the mirror neuron system.

[Reed and McIntosh \(2013\)](#) also argue that social responses involve much more than just reflection as implied by mirror neuron based accounts. They specifically highlight how our mirroring social responses may be modulated by the social context depending on how we judge the other person's actions or displays (e.g., Is the act intentional or otherwise? Is the act emotionally loaded or otherwise?). Hence, they argue for a much richer account of the aetiology of social response than the low-level account offered by much of the mirror neuron literature.

[Williams \(2013\)](#) takes a somewhat different view of the limitations of the low-level account of mirroring. In particular he questions whether the mirror neuron account can be scaled up to deal with the sort of complexity involved in adopting another's pattern of social behaviour and proposes the notion of “portrait” neurons to adequately capture the constructive process of “mirroring” others in socially and cognitively sophisticated ways. He relates these arguments to abnormalities in social responding associated with autism.

(4) Do mirror systems support joint action?

[Colling, Knoblich and Sebanz \(2013\)](#) emphasize how mirror systems support a tight functional link between perception and action. They then go on to ask how these perception-action links might help people to perform actions together. They then discuss three possible functions of mirroring for joint action: 1) supporting temporal coordination in real time, 2) enabling seamless integration of one's own and others' actions in joint action planning, and 3) enabling groups to imitate the coordinated actions of other groups.

[Ondobaka and Bekkering \(2013\)](#) argue for a multi-tiered account of mirroring in which both conceptual and perceptuo-motor information is being taken into account. This framework is motivated by Bayesian inference models (e.g., [Körding & Wolpert, 2006](#)) integrating the conceptual and perceptuo-motor levels of behavioural control. They discuss some recent behavioural evidence in support of this framework.

In trying to explain the interweaving of action and action observation during joint action [Pezzulo \(2013\)](#) also proposes a Bayesian predictive coding framework ([Dindo, Zambuto, & Pezzulo, 2011](#); also [Pezzulo, Iodice, Ferraina, & Kessler, 2013](#), for a physiologically plausible approach). In this notion co-actors' actions become coordinated to jointly minimize prediction error and the “distance” to their common goal, thus, generating shared action plans. In this account mirror systems could optimize inference at multiple hierarchical levels: “how to make my action compatible with yours?” , “what action should I do next?” , and “what action plan should we agree on?”

2. Views and conclusions

After about 20 years of mirror neuron research in monkeys and humans it appears that a simple mirroring mechanism is not sufficient for explaining the origin of the whole plethora of human social perception, cognition and interaction. Even at the simplest level of observing and responding to other's actions, context and high-level goals play an essential top-down role in mediating the ‘mirroring’ process (e.g., imitative vs complementary actions). Furthermore, the true function or even causal role of mirror neurons remains largely unclear (e.g., [Cook and Bird, 2013](#) and [Hamilton, 2013](#); [Heyes, 2013](#) and [Reed and McIntosh, 2013](#)). Nevertheless, the notion of simple, fast and direct associations between what we observe and how we act still has strong theoretical appeal, ranging from precise copying ([Whiten, 2013](#)), to implicit social mimicry (for review see [Niedenthal et al., 2005](#)), and to predicting others' actions in complex joint action scenarios (e.g., [Colling et al., 2013](#), [Ondobaka and Bekkering, 2013](#) and [Pezzulo, 2013](#)).

The origins of mirror mechanisms have been heavily debated over the past decades. Accordingly, several notions are represented in this collection of papers, ranging from evolutionary adaptation ([Gallese, 2013](#) and [Whiten, 2013](#)) to learning by association ([Cook and Bird, 2013](#) and [Heyes, 2013](#), in parts [Barsalou, 2013](#)), while one paper proposes an intermediate notion, where learned mirroring functions may have impacted on natural selection in concordance with the Baldwin effect ([Wilson, 2013](#)).

Based on this collection of papers it also seems important to disentangle the adaptation as opposed to association discussion from another dimension of the debate- the domain-specificity (e.g., [Gallese, 2013](#), [Whiten, 2013](#) and [Williams, 2013](#)) as opposed to domain-generality of mirror neurons (e.g., [Cook and Bird, 2013](#) and [Heyes, 2013](#)). Although “association” appears to be closer to a domain-general and “adaptation” to a domain-specific view, conceptually, there are no 1:1 relationships (e.g., [Wilson, 2013](#)). For instance, depending on the nature of the input provided to an “associator” , the system may result in a more domain-general or a more domain-specific end-state. Simply put, the more variable the input the more domain-general the learned associations would be. Accordingly, more variable input to the MNS in terms of visuo-motor associations during development could result in a domain-general system (e.g., [Heyes, 2013](#), [Newman-Norlund et al., 2010](#), [Ondobaka and Bekkering, 2013](#) and [Press et al., 2012](#)). In contrast, more biased/constrained input, for example due to the isomorphism and correlations between visual bodies and proprioceptive body feedback ([Kessler and Miellet, 2013](#) and [Wilson, 2013](#)), or because of embedding within reoccurring contexts ([Barsalou, 2013](#) and [Myachykov et al., 2013](#)) could result in a more constrained, domain-specific system. Thus, we propose a distinction between domain-general, (highly) domain-specific and “constrained” domain-specific views of human mirroring mechanisms that should be regarded at least in part as independent of the adaptation as opposed to association debate.

Rather than consider only the “nature” of mirror mechanisms in humans and other species, the majority of papers in this Forum also discuss the “meaning” of mirroring mechanisms within the wider context of human social functioning. While some question the adequacy of existing labels such as “motor resonance” , “embodied simulation” , etc. ([Heyes, 2013](#)), others assume a common code between perception and action and explore the

crucial mediating role it might play for complex social activities such as joint actions ([Colling et al., 2013](#), [Ondobaka and Bekkering, 2013](#) and [Pezzulo, 2013](#)) or complex cognitive processes and simulations ([Barsalou, 2013](#) and [Gallese, 2013](#)). They argue that body-based representations may play a crucial role in providing fast, immediately shared or aligned dynamic representations for actors engaged in complex social interactions ([Butterfill and Sebanz, 2011](#), [Colling et al., 2013](#) and [Pickering and Garrod, 2013](#)). They might also feed into shared action plans ([Gallotti and Frith, 2013](#), [Pezzulo, 2013](#) and [Pezzulo et al., 2013](#)), which significantly facilitate joint actions by allowing quick coordination due to predictive coding of other agents' possible actions ([Colling et al., 2013](#), [Ondobaka and Bekkering, 2013](#) and [Pezzulo, 2013](#)). [Hamilton's \(2013\)](#) emphasis on complementary and socially adequate responses further highlights the flexibility needed of mirroring mechanisms if they are to play any significant role in explaining complex human social behaviour - or associated clinical deficiencies (see also [Williams, 2013](#)). However, this stands in stark contrast to the need for precise and highly congruent mirroring when learning by imitation ([Cook and Bird, 2013](#) and [Whiten, 2013](#), for discussion).

Thus, the papers in the Forum reveal the functional range required of human mirroring capacities: high precision for copying others during imitation learning versus high flexibility and complementarity when coordinating or competing with others (also [Pezzulo et al., 2013](#)). [Reed and McIntosh \(2013\)](#) highlight such context-, intention-, or goal-dependency, while [Barsalou, 2013](#) and [Heyes, 2013](#), and [Gallese \(2013\)](#) emphasize (each in their own way) the flexible embedding of mirroring within dynamic cognitive processes, and for (embodied) simulations/representations of the self, others, and the world in general.

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