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Literature review

More than an imitation game: Top-down modulation of the human mirror system

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ABSTRACT

All interpersonal interactions are underpinned by action: perceiving and understanding the actions of others, and responding by planning and performing self-made actions. Perception of action, both self-made and observed, informs ongoing motor responses by iterative feedback within a perception-action loop. This fundamental phenomenon occurs within single-cells of the macaque brain which demonstrate sensory and motor response properties. These 'mirror' neurons have led to a swathe of research leading to the broadly accepted idea of a human mirror system. The current review examines the putative human mirror system literature to highlight several inconsistencies in comparison to the seminal macaque data, and ongoing controversies within human focused research (including mirror neuron origin and function). In particular, we will address the often-neglected other side to the 'mirror': complementary and opposing actions. We propose that engagement of the mirror system in meeting changing task-demands is dynamically modulated via frontal control networks.

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1. Introduction

Perception and action are inextricably linked processes, and together form the basis of every aspect of our experience of and interaction with the world. Of particular importance are the interactions humans have with each other. These require complex, concurrent processes for perceiving the actions of the self and other. Such perceptual representations inform the preparation of corresponding motor responses, through to the execution of the action and the perception of the outcome of this action (known as the perception-action-loop). A phenomenon variously termed *motor resonance* (e.g. Cross and Iacoboni, 2014a), *mirroring* (Rizzolatti and Fogassi, 2014) and *vicarious activation* (Keysers and Gazzola, 2009), has been identified as a critical part of this perception-action-loop. Of course this began with the report of 'mirror neurons' in the premotor cortex of the rhesus macaque, discovered some 20 years ago by Rizzolatti's group (di Pellegrino et al., 1992; Gallese et al., 1996). Mirroring refers to the apparently similar neural processing of observed actions as for self-made actions, particularly within regions of the brain previously thought of as selectively coding motor control, i.e. self-made actions. Critically we avoid a definition based on a strict congruence between observed and executed actions.

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Here we review the human ‘mirror system’ literature to highlight a number of inconsistencies with the original macaque data, and to discuss ongoing controversies within the field. By contrasting various theories of mirror system origin and function, we point to a convergence of views and provide a useful framework from which to pose further questions. In particular, we will address the often-neglected other side to the ‘mirror’, i.e. complementary and opposing action responses, and how an action “mirroring” system might allow alternative task-demands to be met. Some level of ‘mirroring’ may always occur (Kilner et al., 2003), but we argue these representations are propagated depending on prior associations between stimulus and response actions, and the context of the task at hand. Control processes, such as response-selection, conflict detection, and ongoing goal-maintenance can be engaged to gauge the task-relevance of incoming sensory information to optimise the generation of motor responses. Even in situations where stimulus and response actions are not perfectly compatible, the mirrored representations of observed actions may still be usefully integrated to prepare complementary responses. We argue that activation of mirror regions is dynamically adaptive and integrated with the top-down control systems of frontal networks. Cognitive control collectively refers to higher-order executive functions which enable one to coordinate lower-level processing toward meeting internal goals, while remaining flexible to changing demands. (Dosenbach et al., 2008; Koechlin et al., 2003). These processes and the networks underlying them have been reviewed in detail elsewhere (for theoretical review Botvinick et al., 2001; Miller and Cohen, 2003; Ridderinkhof et al., 2004). Here we focus on the influence of cognitive control on dynamic, adaptive and predictive sensorimotor associations in the action-perception and motor-response loop. This view aligns with the associative sequence learning account of mirror neuron development and evolution (Heyes, 2010a), a parsimonious theory for the sensorimotor associations linking the representations of both observed and executed actions. Hence, we apply a system-level framework to sensorimotor mirroring, incorporating existing cognitive and computational models of how the brain optimises behavioural responses to sensory information (Kilner et al., 2007a; Körding and Wolpert, 2004).

2. Mirror neuron to mirror system

How we conceive of action perception and action execution has profoundly changed by the discovery of motor neurons with sensory properties in the ventral premotor region F5 in the macaque monkey, (di Pellegrino et al., 1992; Gallese et al., 1996). The response properties of these cells vary but their distinguishing feature is that their firing is modulated both by action execution and action observation, varying depending on the degree of action specificity. The coining of the term ‘mirror neuron’ describes this unique feature of being responsive to both motor and sensory action-related inputs.

The purported function of mirror neurons is not ubiquitously agreed upon (e.g. Casile et al., 2011; Cook and Bird, 2013; Hickok, 2013). Many researchers refer to mirror neurons as encoding action-goals and subserving action understanding, without clarifying these functions or how such functionality arises. Although much of the monkey physiology data seemed to demonstrate specificity of responses to goal-directed actions (i.e. object-oriented as in picking up food), Ferrari et al. have shown non-goal directed mouth actions (‘communicative’ gestures) to elicit activity in mirror neurons in the monkey pre-ventral cortex (Ferrari et al., 2003). Hence the idea of mirror neurons only responding to goal-directed actions is left wanting (Catmur, 2012). This is not to imply that higher-order cognition about intentions and goals are not influenced by mirror-matching sensorimotor information; however, there is a tendency in the literature to over-simplify the description of ‘mirroring’ and then ascribe extraordinary consequences to this mechanism (Heyes, 2010b; Kilner and Lemon, 2013). This is further confused by hypothesised functions of mirror neurons becoming entangled with explaining the origin of mirror neurons. The genetic account of mirror neurons assumes their fundamental role is action understanding, for which the development of mirror neurons is genetically predisposed due to natural selection pressure favouring this function (Lepage and Théoret, 2007; Rizzolatti and Craighero, 2004). Therefore, the hypothesised function of mirror neurons is offered as an account of the origin of mirror neurons (Cook et al., 2014). This view of mirror neurons was apparently affirmed by neonatal imitation research (e.g. seminal studies Meltzoff and Moore, 1977, 1989; and more recent review chapter: Meltzoff, 2002). However, this line of evidence has been strongly refuted by a recent longitudinal study (Oostenbroek et al. 2016). Epigenetic accounts improve on the rigid genetic perspective by incorporating the influence of learning and experience, while arguing for a level of innate properties upon which experience builds (Bonini and Ferrari, 2011; Ferrari et al., 2013; Giudice et al., 2009). As such, this epigenetic perspective draws nearer to a view of mirror properties being experience-based.

2.1. Experience-based mirroring

The Associative Sequence Learning account of mirror neurons offers a parsimonious explanation for how neurons acquire mirroring properties: sensorimotor associations form based on the experience of contingent and repeated activation of a sensory and a motor representation of a particular action (Catmur, 2012; Catmur et al., 2009; Cook et al., 2014; Heyes, 2013, 2010a, 2016; Hickok and Hauser, 2010). Being experience-based, such connections are adaptable which allows for a wide variety of sensory inputs to mirror neurons. These then code for particular motoric responses experienced in contingent relationships with a certain range of effective sensory inputs over the course of an individual’s learning history (Catmur, 2012). The domain-general process of associative learning allows for mirror neurons to make contributions to action understanding and social cognition but does not assume this (Cook et al., 2014). From this perspective mirroring may be active for imitation without being *for* imitation (Brass and Heyes, 2005; Hickok, 2013). Thus action understanding can take advantage of automatic imitation without precluding experience-based changes in sensorimotor associations and context-dependent inhibition of imitative tendencies.

A complementary account of mirroring is the Hebbian learning model proposed by Keysers et al. (Keysers and Gazzola, 2014; Keysers and Perrett, 2004). Based on anatomical connectivity of the macaque brain, Keysers summarises the mirror circuitry as a series of reciprocal connections between area PF of the inferior parietal lobule and both premotor area F5 and the superior temporal sulcus (STS, Keysers and Perrett, 2004). All three of these areas respond to the sight of another agent’s action, but only areas PF and F5 also respond to the monkey’s self-generated actions. To explain the mirror properties of F5 and PF, Keysers and Perrett apply the Hebbian learning rule of consistent repeated cell-firing increasing the efficiency of synaptic connections between pre and post-synaptic cells, and thus leading to spike-timing dependent synaptic plasticity. Importantly in their model of STS-PF-F5 circuit, the STS functions to cancel out the agent’s own movements based on temporal correlations between visual, auditory and motor representations occurring during the action observation and self-made action execution. It is hypothesised that a similar feedback loop exists in the human neocortex, between homologue regions (Keysers and Gazzola, 2014). These two perspectives, Hebbian and associative, are not mutually