



## Review

# The contribution of brain sub-cortical loops in the expression and acquisition of action understanding abilities<sup>☆</sup>



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## ABSTRACT

Research on action understanding in cognitive neuroscience has led to the identification of a wide "action understanding network" mainly encompassing parietal and premotor cortical areas. Within this cortical network mirror neurons are critically involved implementing a neural mechanism according to which, during action understanding, observed actions are reflected in the motor patterns for the same actions of the observer. We suggest that focusing only on cortical areas and processes could be too restrictive to explain important facets of action understanding regarding, for example, the influence of the observer's *motor experience*, the *multiple levels* at which an observed action can be understood, and the *acquisition* of action understanding ability. In this respect, we propose that aside from the *cortical* action understanding network, *sub-cortical processes* pivoting on cerebellar and basal ganglia cortical loops could crucially support both the expression and the acquisition of action understanding abilities. Within the paper we will discuss how this extended view can overcome some limitations of the "pure" cortical perspective, supporting new theoretical predictions on the brain mechanisms underlying action understanding that could be tested by future empirical investigations.

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## 1. Introduction

In the last two decades, the study of action understanding in cognitive neuroscience has been revolutionized by the discovery of mirror neurons (Rizzolatti et al., 2001; Rizzolatti and Craighero,

2004; Lestou et al., 2008; Evangelou et al., 2009; Bonini and Ferrari, 2011). Mirror neurons were first discovered in the monkey pre-motor area F5 (Di Pellegrino et al., 1992; Rizzolatti et al., 1996). Subsequently they were also found in the inferior parietal lobe (Fogassi et al., 2005; Gallese et al., 2002), in particular in area PFG (Rozzi et al., 2008; Bonini et al., 2010). The distinctive feature of these neurons is that they are activated when monkeys perform an action and also when they observe a similar action executed by another subject. Neuroimaging evidence suggests that mirror neurons might exist in homologous areas of the human brain (Buccino et al., 2001; Grèzes et al., 2003; Rizzolatti and Arbib, 1998; see also Mukamel et al., 2010 for a recent single cells recording in human patients with intractable epilepsy).

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There is now a growing consensus that mirror neurons are part of a wider “action understanding network” in the monkey and human brain which, at minimum, encompasses the bilateral posterior superior temporal sulcus (STS) and adjacent middle and superior temporal gyri (MTG, STG, respectively), the inferior parietal lobule (IPL), inferior frontal gyrus (IFG), dorsal premotor cortex (PMd) and ventral premotor cortex (PMv) (Grafton and Tipper, 2012; Caspers et al., 2010; Cattaneo and Rizzolatti, 2009; Rizzolatti and Craighero, 2004). Within this cortical network, one hypothesis is that mirror neurons implement a “direct resonance” or “direct matching” mechanism according to which the observed action is “reflected” in the motor patterns for the same action of the observer (Buccino et al., 2004; Uithol et al., 2011). A related hypothesis, called “simulation theory” (Gallese and Goldman, 1998), is that embodied simulations support the encoding of perceived actions based on one’s own motor repertoire (see also Prinz, 2006; Pezzulo, 2011; Pezzulo et al., 2013; Wilson and Knoblich, 2005; Wolpert et al., 2003 for related theories emphasizing prediction).

Three main issues feed the discussion about the limits of the mirror mechanism in explaining action understanding. First, how do the *motor abilities of the observer* and the *environmental constraints* contribute to action understanding? Both the cortical direct matching hypothesis and the simulation theory suggest that action comprehension crucially relies on the ability to produce the same action. However, these mechanisms alone might not be sufficient to support the understanding of actions that the perceiving agent cannot produce (Calvo-Merino et al., 2006; Press et al., 2011a). As an alternative to simulation theory, the “teleological theory” connected to it describes action understanding as an inferential process that operates over the target goal and the environmental constraints (contextual information) that might facilitate or limit the goal achievement. Although the result of this process may activate the motor system, the process in itself depends on non-motor mechanisms and then extends naturally to actions outside the motor repertoire of the perceiver agent (Csibra, 2003). In the same line, others have proposed that motor phenomena during action observation could be epiphenomenal rather than causal, and that detecting motor system activity during action observation does not license the conclusion that motor system is causally involved in action understanding (Mahon and Caramazza, 2008). They claim that it might be equally plausible that action understanding involves mainly perceptual processes and that, once action is understood, it activates the motor system which provides the information on how to (eventually) perform the action.

Second, the cortical mirror mechanism conceived as direct-matching and the simulation theory alone might not be sufficient to account for the *different levels at which an observed action can be understood* (Ramnani and Miall, 2004; Kilner, 2011). Action representations in the brain, indeed, are organized at multiple hierarchical levels and, as a consequence, there are multiple levels at which the observer could understand them (Hamilton and Grafton, 2007; Thill et al., 2013). As one moves up the hierarchy, the action is represented in more abstract terms (Kilner et al., 2007; Kilner, 2011; Pezzulo and Dindo, 2011). In particular, the kinematic aspects of a movement related to the trajectory and to the velocity and the motor aspects related to the muscle activity could be considered at the bottom of the action representations hierarchy, whereas the aspects related to the goal of the action (the purpose of the action, e.g., grasp an object) and to the intention of the action (the overall reason, e.g., grasp an object to eat) could be considered at the top of the hierarchy. A clear hypothesis on how the mirror neurons deal with action understanding at any level of complexity of action representation is still missing (Kilner, 2011). In the past some authors suggested a classification of mirror neurons based on different aspects of action representations analyzing the single neuron activation in primates. Gallese and colleagues (Gallese et al., 1996),

for example, recorded the electrical activity from 532 neurons in the rostral part of inferior area 6 (area F5) of two macaque monkeys and used as a classification criterion the congruence between the executed and observed motor acts effective in triggering them, to split the mirror neurons into two main classes: strictly congruent and broadly congruent mirror neurons. Strictly congruent mirror neurons discharge when the observed and executed effective motor acts are identical both in terms of goal (e.g., grasping) and in terms of the way in which that goal is achieved (e.g., precision grip), whereas to be triggered broadly congruent mirror neurons require similarity but not identity between the observed and executed effective motor acts (Fabbri-Destro and Rizzolatti, 2008; Gallese et al., 1996). Some authors suggest that within the mirror circuit premotor and parietal areas could be respectively involved in the dissociable processing of abstract goals and movement representation at the kinematic level (Iacoboni et al., 2001; Iacoboni, 1999), whereas others suggest processing of action goals independent of motor trajectories in the parietal cortex (Fogassi et al., 2005; Hamilton and Grafton, 2006) and unexpected intentional actions in the STS (Saxe et al., 2004; Pelphrey et al., 2004). Molnar-Szakacs et al. (2006), for example, used fMRI to investigate the role of the fronto-parietal human mirror neuron system in representing hierarchical complexity during the observation of object-directed action sequences. They found that activity in mirror neuron areas varied according to the motoric complexity of the observed actions, but not according to the developmental sequence of action structures. Their results show how the fronto-parietal mirror neuron system provides a fairly accurate simulation process of observed actions, mimicking internally the level of motoric complexity. Finally, a further proposal suggests a two-pathway model to understand more abstract actions (those related to goals and intentions) that also involves ventral regions beside the traditional mirror circuit (Kilner, 2011; Press et al., 2011b). According to this view multiple possible actions are selected and processed during action observation, but one is represented more strongly than the others.

A third important issue regards the *acquisition* of the action understanding capacity. This point is crucial since a substantial part of the mirror circuit functioning might be related to the need to support the acquisition of action understanding ability and not only its expression. This claim is in line with the general idea that much of the structure and organization of the brain depends on the fact that behaviour has to be acquired, and not only expressed (Büchel et al., 1999; Xu et al., 2009; Bassett et al., 2010; Anderson, 2010; Caligiore et al., 2010).

The *associative sequence learning model* (ASL) proposes that we are not born with a mirror neuron system (Heyes, 2010). Rather, the mirror properties of mirror neurons emerge through *sensorimotor associative learning* where the natural correlation between observation of an action and its execution establishes excitatory links between sensory and motor representations of the same action. In this way, representations that were originally motor become mirror, that is activated when observing and executing the same action. According to the ASL hypothesis mirror neurons, as a by-product of associative learning, could play a part in action understanding but they do not develop for action understanding (Heyes, 2010; Press et al., 2011b). In contrast, some authors have recently proposed that the ASL hypothesis could support an explicit role of mirror neurons in action understanding if the hypothesis is considered within the *predictive coding* (PC) framework (Kilner et al., 2007; Urgesi et al., 2007). The PC proposal pivots on the *hierarchical anatomical and functional organization* of the cortical mirror circuit (STS, PFG, F5; Fig. 1a). According to the PC hypothesis, the activity within one level of the hierarchical organization of actions within the mirror circuit (Hamilton and Grafton, 2007) acts as a prior constraint on sub-ordinate levels. For example, contextual

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