

Mirror mechanism and dedicated circuits are the scaffold for mirroring processes

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Abstract: In the past decade many studies have demonstrated the existence of a mirror mechanism that matches the sensory representation of a biological stimulus with its somatomotor and visceromotor representation. This mechanism, likely phylogenetically very old, explains several types of mirroring behaviours, at different levels of complexity. The presence in primates of dedicated neuroanatomical pathways for specific sensorimotor integrations processes implies, at least in the primate lineage, a hard-wired mirror mechanism for social cognitive functions.

The core issue of the target article is whether mirror neurons (MNs) arise by associative learning. My comments, based on neuroanatomical and electrophysiological expertise, focus on this and other related issues (mirror mechanism and action understanding) addressed by the article.

The mirror neuron mechanism. The most important aspect of MNs is their capacity to match the visual/acoustic cortical representation of a biological stimulus with its corresponding somatomotor or visceromotor representation. Thus, MNs constitute a mechanism that not only explains the automatic decoding of the motor acts of others, but also many other types of processes involved in social cognitive functions (e.g. emotion recognition, imitation, oro-facial communication). Recent studies have shown the existence of MNs active during both listening and production of species-typical song in singing birds (Prather et al. 2008), suggesting that mirror mechanisms are probably very primitive solutions evolved in different vertebrate classes to elaborate sensory information for social cognition. Furthermore, behavioural evidence suggests that other vertebrates such as rats or dogs (Range et al. 2007; Zentall & Levine 1972) or even invertebrates such as the octopus (Fiorito & Scotto 1992), could be endowed with some form of mirror mechanism.

By using the same matching mechanism, mirroring may occur, even within the same species, at different levels: in the comprehension of goals (Cattaneo et al. 2009; Fogassi et al. 2005; Rizzolatti et al. 2004) or of meaningful communicative or symbolic gestures (Ferrari et al. 2003; Lui et al. 2008) (high level), and in the decoding of observed movements rather than of motor acts (Catmur et al. 2007; Fadiga et al. 1995) (low level).

Mirror neurons and sensorimotor associative learning. Cook et al. claim that MNs are the result of associative learning rather than an adaptation selected by evolution for action understanding genetically coded in humans and ancestors. Following the authors' reasoning, if we knew the experience of every monkey since birth, we could predict the formation, in monkeys living in different developmental environments, of different types of MNs. Furthermore, many of the typical primate behavioural functions of daily life would be the result of associative learning, and therefore we should observe a large inter-individual behavioural variability. However, it is well known that, for example, object- or space-related sensorimotor transformations for reaching-grasping actions are grounded on dorsal cortical circuits (Rizzolatti & Matelli 2003) that are phylogenetically very old and, in the primates' lineage, very similar among different species. Just as there are these dedicated circuits, linking specific parietal and premotor areas (Rizzolatti & Luppino 2001), so there is also a dedicated *mirror circuit* for hand actions observation, linking anterior superior temporal sulcus (aSTS)↔inferior parietal cortex (PPG)↔ventral premotor cortex (area F5c) (Nelissen et al. 2011, p. 3754). It is evident that such selected circuits cannot re-build every time. They provide, rather, the

neuroanatomical scaffold for both hard-wired and newly-learned sensorimotor transformations. In these circuits, pre-existing and new motor representations are matched with their corresponding sensory representations.

As an example of an anatomico-functional circuit in which the mirror matching mechanism operates, a series of recent works (Bonini et al. 2010; Fogassi et al. 2005) has shown that the discharge of purely motor and MNs of monkey premotor (area F5c) and parietal (area PFG) cortex is modulated, during grasping observation/execution, depending on the behavioural goals of specific executed or observed action sequences (grasp-to-eat or grasp-to-place). Furthermore, the percentage of MNs tuned for the hard-wired action (grasp-to-eat) is much higher than that of MNs tuned for the learned action (grasp-to-place). Overall, these and other data suggest that the mirror mechanism, deeply rooted in primate evolution, also plays a strong role in the extension of action understanding capacity to new actions, in motor skill consolidation (Cross et al. 2006) and in observation-based rehabilitation (Ertelt et al. 2007). These processes could also benefit from associative learning.

Action recognition and action understanding. Cook et al. claim that there is no consensus on the concept of action understanding and on its distinction from action perception and recognition. If the objective of the nervous system were to simply ensure action recognition, probably the visual system would be enough: some sectors of aSTS would be the best candidate for recognizing the actions of others. However, if we assume that the motor system is crucial for cognition because it provides information about motor goals, aSTS areas alone are not able to support action understanding because they do not show motor responses (Perrett et al. 1989). Thus, we can hypothesize that the reciprocal neuroanatomical links between high-order visual areas and motor areas endow individuals with two main abilities: (1) to interpret the vision of a hand approaching an object in terms of goal; (2) to better perceive the details of the observed actions.

Two recent studies support these two functions. The first (Caggiano et al. 2009) shows that in half of recorded MNs the intensity of the visual response is different depending on whether the observed grasping is performed within or outside the peri-personal space of the monkey, and this effect can be further modulated by the possibility for the monkey to act or not in its peri-personal space. The second (Caggiano et al. 2011) shows that 75% of the recorded MNs discharge more strongly when the monkey sees the action either from an egocentric or a third-person perspective. These results can be interpreted as the demonstration that MNs, although always encoding, in their output, the goal of a motor act (they are basically motor neurons), can, at the very same time, in conjunction (through feedback projections) with high-order visual areas sensitive to biological stimuli, provide information on specific details of the observed action, by enhancing the activity of the sensory neurons that are more selective for those details.

Understanding action with the motor system

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Abstract: We challenge Cook et al.'s claim about the vagueness of the notion of action understanding in relation with mirror neurons. We show the multidimensional nature of action understanding and provide a definition of motor-based action understanding, shedding new light on

the various components of action understanding and on their relationship. Finally, we propose an alternative perspective on the origin of mirror neurons, stressing the necessity to abandon the dichotomy between genetic and associative hypotheses.

The role of the mirror mechanism (MM) in social cognition is still a matter of debate. Much disagreement is primarily due to different notions of action and of action understanding. On the standard view, an action is directed to a goal in virtue of the action's being appropriately related to some high-order mental states (e.g., beliefs, desires, and intentions) representing this goal. The relation between actions and their goals is traditionally assumed to be largely independent of the motor processes and representations underpinning action execution. These processes and representations allegedly concern motor features such as joint displacements or muscle contractions only. However, two decades of cognitive and neuroscientific research on the cortical motor system has repeatedly challenged this view. Neurophysiological and behavioral evidence (Rizzolatti & Sinigaglia 2010) has demonstrated that motor processes may involve motor representations of action goals (e.g., to grasp, to place, etc.), and not only kinematic or dynamic components of actions. This suggests that beliefs, desires, and intentions are neither primitive, nor the only bearers of intentionality in action. Indeed, motor representation is enough to ground the directedness of an action to its goal (Gallese 2000; Butterfill & Sinigaglia 2014).

The MM indicates that this holds not only for action execution, but also for action observation. The activation of the MM can be selectively related to the observed action goal regardless of its kinematics, dynamics, and the body effector involved (Gallese & Sinigaglia 2011; Rizzolatti & Sinigaglia 2010). This supports the claim that the MM may play a role in action understanding. By recruiting her own motor representation of the goal to which the observed action is directed, the observer may understand what the agent is doing without needing any high-order processing.

Claiming that the MM plays a role in action understanding of course does not imply that action understanding is overall solely explained by the MM. Understanding an action is a complex process. It involves at least representing to which (proximal and distal) goals the action is directed; identifying which beliefs, desires, and intentions specify reasons explaining why the action happened; and realizing how those reasons are linked to the agent and to her action. The MM enables the representation of the goals of others' actions by taking advantage of one's own motor cognition. The richer a person's own motor cognition is, the greater her sensitivity to another's action and the better her ability to grasp the goal to which that action is directed. Consistently, action understanding deficits occur following specific impairments in the recruitment of the motor representation of action goals (for a review, see Gallese & Sinigaglia 2011).

The fact that a motor-based action understanding doesn't match any "established category of psychological functioning" (target article, sect. 9.1) is not per se a good reason to reject it. On the contrary, it provides a new empirically and theoretically sound framework to investigate basic aspects of social cognition. Furthermore, differently from what Cook et al. maintain, it enables us to shed new light on the various components (e.g., perceptual, motor, and mentalizing) of action understanding, as well as on their relationship. To this extent, it is worth noting that even high-order purely sensory mechanisms, like those characterizing extrastriate cortices such as the Superior Temporal Sulcus (STS) region, are insufficient to represent the goal of a given action at the same general level as the MM does. In addition, there is no evidence to date that the STS responds both to proximal goals (e.g., grasping a piece of food) and to distal action goals (for eating or for throwing away), as the MM does (Gallese & Sinigaglia 2011; Rizzolatti & Sinigaglia 2010).

Pertaining to the relationship between the motor components of action understanding and mentalizing, many studies have

demonstrated that the MM kicks in when people have to understand to which goal an observed action is directed (de Lange et al. 2008; Liepelt et al. 2008a). When people must determine the reasons why an agent performed a given action, additional activations of cortical regions such as the mesial anterior frontal cortex, the anterior cingulate cortex, and the temporo-parietal junction – typically considered to belong to the so-called mentalizing network – are detected (de Lange et al. 2008; Liepelt et al. 2008a; Van Overwalle 2009). In spite of many theoretical attempts to integrate these different components of action understanding, so far there is neither convincing evidence about the mentalizing specificity of these activations, nor a theoretically coherent and empirically motivated explanation of how the "mentalizing network" might work. Ironically, such controversial aspects of the neurobiological bases of mentalizing have not attracted so much debate, certainly not as much as the role of the MM in social cognition.

Finally, the functional properties of the MM and its involvement in action understanding are not captured by either a strictly genetic or a purely associative account about its origin. We hypothesize (Gallese et al. 2009) that an innate rudimentary MM is already present at birth, which can then be flexibly modulated by motor experience and gradually enriched by visuomotor learning. Indeed, such a system could be an ideal candidate for the neural underpinning of neonatal facial imitation in humans and nonhuman primates. Recent neurophysiological evidence also suggests there is an inborn rudimentary form of action mirroring in neonate rhesus macaques (Vanderwert et al. 2013). Differently from the associative account proposed by Cook et al., our hypothesis entails a primacy of motor experience in the development of the MM and its contribution to understanding others' actions. This primacy is supported by several studies showing a causal link between the ability to produce an action and the ability to understand it (see, among others: Cannon & Woodward 2012; Kanakogi & Itakura 2011).

Evolution after mirror neurons: Tapping the shared manifold through secondary adaptation

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Abstract: Cook et al. laudably call for careful comparative research into the development of mirror neurons. However, they do so within an impoverished evolutionary framework that does not clearly distinguish ultimate and proximate causes and their reciprocal relations. As a result, they overlook evidence for the reliable development of mirror neurons in biological and cultural traits evolved to work through them.

Cook et al. have done a great service by marshaling the mounting evidence that experience influences the operation of mirror neurons (MNs). This work reinforces other recent calls (e.g., Henrich et al. 2010) to study the effects of variable environments, both in humans (across cultures) and in nonhuman primates (across rearing and field settings), on the development of neural and psychological systems. Cook et al. advance this issue with the hypothesis that specific aspects of developmental environments influence the ontogeny and functions of MN systems. Encouragingly, anthropologists have documented relevant population variation, including in adult interactions with infants (e.g., Ochs & Schieffelin 1984), and in interactive practices across