A curious book on mirror neurons and their myth

Review of Gregory Hickok's "The Myth of Mirror Neurons: The Real Neuroscience of Communication and Cognition"

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“You can fool all the people some of the time, or some of the people all the time, but you cannot fool all the people all the time.” This famous sentence attributed to Abraham Lincoln seems to be contradicted by the fascination that neuroscientists, philosophers, sociologists, psychologists, actors, journalists, and even novel writers have with mirror neurons since their discovery. The aim of the book by Hickok (“The Myth of Mirror Neurons”) is to dispel this fascination and show that mirror neurons are neurons not different from many others and, as such, they do not deserve any particular attention.

The book is rather bizarre. It is easy to read and sometimes conveys interesting ideas. However, the core of the book -the criticism of mirror neurons- is superficial and mainly based on ill-digested notions of neuroscience and neuropsychology. Furthermore, while the author quotes the old mirror neuron literature (that of the last century!) extensively, he ignores most of the recent findings coming from Parma (see Rizzolatti et al 2014) and other laboratories like Leuven (e.g. Nelissen et al., 2011; Abdollahi et al., 2013), Tübingen (e.g., Caggiano et al 2009; 2011; 2012) and London (Kraskov et al., 2009; Vigneswaran et al., 2013). For most of the book, Hickok’s line of criticism is more like a lawyer’s harangue in a serial like “Law and Order” than a serious scientific refutation.

The author starts with a long list of functions in which mirror neurons are considered to be implicated and it seems to ask to a hypothetical jury: Is it plausible, ladies and gentlemen, that all these functions are performed by a small set of neurons, discovered in the premotor cortex of the monkey brain? The answer is obviously: NO. The point, however, hidden from the hypothetical jury is that mirror neurons of the monkey premotor cortex are only just *one* example of a large number of neurons endowed with *the* *mirror mechanism*. Neurons with mirror mechanism are present in birds (Prather et al., 2008; Keller & Hahnloser, 2009), marmosets (Suzuki et al., 2014), monkeys (Gallese et al., 1996; Rizzolatti et al., 1996), and in several cortical areas of human beings (see for a review Rizzolatti et al., 2014). Mirror neurons that fire when a bird sings or hears the same song have functions obviously different from mirror neurons of the insula activated when disgust is elicited by natural stimuli or triggered by the observation of a disgusted grimace (Wicker et al., 2003); similarly, neurons in Broca's area, triggered by phonemes (Fadiga et al., 2002) have functions different from mirror neurons involved in others' action processing in monkey premotor cortex (see Rizzolatti et al., 2014). *The mirror mechanism is a very general, widespread mechanism transforming sensory information into a motor format. According to where neurons endowed with this mechanism are located, their functions change.* The mirror mechanism may underlie, therefore, the recognition of songs in birds or the sharing of others' emotions in humans, the understanding of action goals in macaque monkeys (and humans) or the recognition of phonemes in humans. Within limits, the mirror mechanism might be compared to fundamental mechanisms such as, for example, excitatory (EPSP) or inhibitory (IPSP) postsynaptic potentials. Nobody is surprised that EPSPs are present in vision and in audition and that they are fundamental for motor activity as well for space perception. If the same logic is applied to the mirror mechanism, one should be not surprised that so many diverse functions are mediated by this mechanism.

A second point raised by Hickok in order to convince the hypothetical jury of how foolish the Parma group is (for they are the main villains of the story) concerns action understanding. Rephrasing Hickok, the question he poses is the following: Is it possible to claim that all actions we observe are understood in virtue of a motor mechanism? We do not fly, and yet we recognize when a bird flies. To speak of the mirror mechanism as the basis of action understanding is mere nonsense. The point, hidden again from the hypothetical jury, is that nobody either in Parma or in any of the thousand papers on mirror mechanism published around the word ever put forward such a claim.

The claim of Rizzolatti and his coworkers from the early days of the mirror neurons discovery was that the mirror mechanism plays a fundamental role in understanding actions that belong to the observers' *motor repertoire*. This point was experimentally addressed in an fMRI experiment (Buccino et al., 2004). It was shown that actions that are present in the observer's motor repertoire (e.g. biting) activate the observer's mirror mechanism regardless of whether they are performed by a dog, a monkey or a human being. Barking does not belong to human motor repertoire and therefore does not activate the human mirror system. Its understanding requires, after activation of visual areas, inferential processes. This duality of action understanding (see Frith & Frith, 2006) has important social and philosophical consequences (for a discussion of this issue see Rizzolatti & Sinigaglia, 2010).

One may still wonder, however, how it is possible that the motor system, which according to classical, nineteenth-century physiology encodes movements, might play a role in action understanding. This claim would be indeed utterly bizarre, if one would believe, as Hickok does, that this is the way in which the motor system works. Actually, the organization of the cortical motor system is much more complex than was believed even 30 years ago (see Rizzolatti & Kalaska, 2012). There is clear evidence that a large number of neurons in the posterior parietal cortex, premotor areas, and even, at a lesser degree in the primary motor area (M1 or F1) encode motor acts, that is movements with a goal and not simple movements (joint displacement). The premotor cortex contains, in fact, what has been named a "vocabulary" of motor acts, which includes (for example in monkeys area F5) acts such as grasping, holding, tearing and placing (Jeannerod et al., 1995). Premotor neurons encoding grasping may discharge during goal achievement accomplished with natural effectors (e.g., the right hand, the left hand or the mouth; see Rizzolatti et al., 1988) or even with artificial implements (e.g., a "reverse" pair of pliers, which requires a sequences of movements opposite to the natural one; see Umiltà et al., 2008). It does not matter which movements are used for achieving the goal, what matters is the goal of the motor act. This property also holds for mirror neurons.

According to Hickok the mirror theory is a child of the motor theory of speech perception, and therefore it *must* be wrong. Actually, while the ideas of Alvin Lieberman (see for instance Liberman & Mattingly, 1985) certainly helped Parma scientists in formulating the mirror theory of action understanding, the theoretical proposal was based on previous findings (as described above) on cortical motor organization: namely, that neurons in the ventral premotor cortex encode motor acts and not simply movements. The sensory-motor transformations mediated by the mirror mechanism in the premotor cortex occur, mostly, at the level of the goal common to the observed and actively executed motor acts.

Neurons are not volatile creatures. If a neuron encodes "grasping" when is activated by the desire of his owner to grasp a piece of bread, it also encodes "grasping" when it is activated by the observation of a person grasping a piece of bread. The neuron cannot in this last case encode "jump". Besides anatomical considerations, which account for this specificity, this is shown by single neuron studies (Gallese et al., 1996; Rizzolatti et al., 1996) and brain imaging experiments (e.g. Gazzola & Keysers, 2009, see for review Caspers et al., 2010; Molenberghs et al., 2012; Rizzolatti et al., 2014 et al.) demonstrating that the same populations of neurons that encode "grasping" during action execution also encode "grasping" during action observation. fMRI studies have shown that the same occurs during motor imagery (Jeannerod, 2001; 2006). When I imagine myself grasping a piece of bread, the same neuronal populations become active as those that are active when I am preparing that action. Neurons do not change their mind about what they will encode. "Grasping" neurons say encode "grasping" regardless of whether they are endogenously or exogenously triggered.

As a good lawyer who uses all the weapons he has for convincing the jury that he is right, Hickok presents (rather surprisingly considering his criticism of associationism in another chapter of the book) some experiments carried out by Heyes and colleagues (Catmur et al., 2007; Catmur et al., 2011). According to Hickok, they show the functional irrelevance of mirror neurons. However, Heyes's experiments were explicitly designed to investigate the origin of the mirror mechanism, not its function in cognition. Here is the main experiment carried out by Heyes and colleagues (Catmur et al., 2011). Subjects were instructed to respond as fast as possible to the observation of a finger movement with another different finger movement ("counter-mirror training"). Heyes and colleagues found that, after the "counter-mirror" training, the motor responses to action observation, evaluated using a TMS, displayed an inverted mapping relative to the original response. Cattaneo and colleagues (Barchiesi & Cattaneo, 2013) subsequently repeated this study, applying stimuli early and late following stimulus onset. They found that, in an early time, training didn't influence participants' responses. Only in a later time segment (at 320 ms) did the responses become "counter-mirror", as in Heyes's study (see also Ubaldi et al., 2013). This suggests that two neural mechanisms may concur in producing motor responses to action observation: a fast and stable system (the mirror mechanism) not influenced by arbitrary visuo-motor associations and a slower mechanism (most likely related to cognitive decisions) that can establish arbitrary associations between visual cues and motor responses.

As well as lacking theoretical relevance, the findings of Heyes and colleagues do not really have to do with the role of mirror neurons in action understanding, the theory criticized by Hickok. Their concern is only the relationship between observed and executed stereotyped finger movements, without investigating the motor processing of more general action goals, such as the grasping of an object or the pushing away of it, which typically feature in goal ascription. The experiments by Heyes and colleagues may challenge some details of the ideo-motor theory of imitation, but they do not bear directly on the mirror mechanism-related action understanding. The evidence, however, in favour of ideo-motor theory of imitation is extremely solid and convincing (Prinz, 1997; Meltzoff & Prinz, 2002). Nobody believes today that imitation is the result of mere association processes. On the contrary it is widely accepted that imitation is based on "shared representational resources for perception and production in the action domain".

Although the "attacks" of Hickok to the role of the mirror mechanism in cognitive functions are mostly naive and superficial, there is one criticism that deserves some attention. This is when he raises the issue of whether a set of premotor neurons can be indeed responsible for such a complex cognitive function like action understanding. If mirror neurons were located in a dish, admitting that you can activate them in a dish, the answer would be certainly not. The crucial point is that action understanding is not determined, as Hickok believes, by the activation of mirror neurons as such, but by the activation of the *mirror mechanism* of which they are endowed, i.e. by their capacity to transform sensory information concerning the observed action into a motor representation of the goal to which that action is directed.

This transformation *ignites* the activity of a complex cortical and subcortical network. This network includes other premotor areas (see Caspers et al., 2010; Molenberghs et al., 2012; Rizzolatti et al., 2014), the basal ganglia (Alegre et al 2010) and the corticospinal motor neurons located in area F5 (Kraskov et al., 2009) and in the primary motor cortex (F1) (Vigneswaran et al., 2013). Thus, the same motor representation that occurs in our brain when we are about to grasp a piece of bread also occurs when another person is grasping it. This commonality between the core neural structures activated by seeing someone else grasping and those activated by our actual grasping (or by our imaging to grasp), is at the basis of the claim that the activation of the mirror mechanism plays a fundamental role in action understanding, (provided, of course, that the observed actions are in our motor repertoire).

This is, however, not the whole story. Considering the massive connections that the premotor cortex has with the parietal lobe, the activation of the premotor mirror neurons may also activate, through a top-down mechanism, the inferior parietal lobule neurons (where there is a large population of mirror neurons; Fogassi et al., 2005), as well as some of the visual areas located in the superior temporal sulcus (STS) region (for a description of the whole hand grasping mirror circuit in the monkey see Nelissen et al., 2011). Top-down influences have been postulated by Caggiano et al. (2011) to explain some properties of F5 mirror neurons and are at the basis of the theory of Kilner and colleagues (Kilner et al., 2007; Kilner, 2011) on the role of mirror neurons in action understanding. Taken together, the bottom-up and top-down activations clearly show that the understanding of others' actions does not involve, as Hickok suggests we claim, only a relatively small set of premotor neurons, but a large network including several motor and sensory areas.

Hickok, after a passionate defence of complex circuits as a neural basis for psychological functions (and the consequent obvious irrelevance of mirror neurons for this role), abruptly changes his mind and in the same chapter suggests that high-order visual neurons, like those located in the STS, can do the job of encoding others' actions and goals.

No doubt that STS cells have an important role in encoding biological movements and even goal-related motor acts (Perrett et al., 1989). However, to date there is no evidence that these cells are able to generalize the goals of the observed action in the same way as the premotor (and parietal) mirror neurons. Furthermore, theoretical reasons make it very implausible that STS neurons may generalize action goals--a fundamental process in action understanding.

To illustrate this point, consider an STS neuron that selectively encodes the visual features of a grasping hand. This neuron, in virtue of a mere visual association, could also, in theory, respond to the visual features of some temporally and spatially proximal body movements. But how could this neuron encode the visual features of a mouth action directed to the same goal (e.g. grasping)? Such a goal generalization is something that goes beyond a possible visual association even when occurring in a higher-order visual region such as the STS. This lack of generalization was nicely demonstrated empirically by a TMS adaption study by Cattaneo et al., 2010. Things are completely different with the premotor and parietal mirror neurons, some of which selectively encode an action goal such as grasping irrespective of the body effector involved in achieving it.

These findings provide a further argument for claiming that the mirror mechanism plays a fundamental role in action understanding. By 'action understanding' philosophers, psychologists and cognitive neuroscientists often indicate concepts that are widely different one from another. They range from goal ascription (that is, the process of identifying the goal to which an action is directed) to belief and desire attribution, and even to complex forms of practical reasoning concerning on one's own or others' actions and thoughts. Some years ago we discussed these issues and distinguished between *understanding goals* and *reasoning* about others' actions and thoughts (e.g. beliefs, desires, intentions). In those studies work we provided theoretical and experimental arguments for a specific role of the mirror mechanism in understanding the goals of others' actions (Rizzolatti & Sinigaglia, 2010; Sinigaglia & Rizzolatti, 2011). This does not rule out the possibility that the mirror mechanism might also affect belief and desire attribution, or even more complex forms of practical reasoning about others' actions and thoughts. However there are as yet no empirical studies, which addressed this issue.

In the work mentioned above we also characterized what is special about the goal understanding based on the mirror mechanism, introducing the notion of '*understanding action from the inside*' (Rizzolatti & Sinigaglia, 2010; Sinigaglia & Rizzolatti, 2011). Far from being a weakening of the previous mirror theory, as Hickok thinks, this notion indicates and stresses the difference between an associative and a motor-based understanding of others' actions. According to this notion, recruiting our own motor representations of observed actions allows us to capture the goals of these actions as motor possibilities, 'from the inside', that is as something to which our actions are directed, and not just 'from the outside' as something which can happen, as one event (even a physical one, like the falling of an apple) among others.

A way of providing evidence for a difference between understandings 'from the inside' and 'from the outside' is to compare people who are solving a goal understanding task by capitalizing on their own motor resources or just using the visual information concerning the others' actions. Lack of the relevant motor expertise makes people slower and less accurate in anticipating the action goals and understanding what is going on (Casile & Giese, 2006, Aglioti et al., 2008). These differences in response time and in accuracy reflect different heuristics (i.e. using one's own motor ability to act or relying on visually based inferences) in solving the understanding goal tasks (Boria et al., 2009). This is in line with a series of studies demonstrating that transient lesion of the premotor areas (determined by repetitive TMS) (see, for instance, Urgesi et al., 2007; Costantini et al., 2014; Michael et al., 2014; see fore review Avenanti et al., 2013) or clinical lesions of motor areas endowed with the mirror mechanism determine deficits in action recognition. This is true in the case of damage of the parietal as well as the premotor areas (for a review see Rizzolatti et al., 2014, Urgesi et al., 2014).

Hickok is sceptical that clinical lesion data support the claim that there is a role for the mirror mechanism in action understanding. The main reason for his scepticism is that the deficit in action understanding is typically not complete, being sometimes mild, and does not necessarily affect all patients in the same way. According to Hickok, if motor areas endowed with mirror properties were really relevant for action understanding, their lesions should result in a kind of blindness for others' actions and goals. If you take this objection seriously, you have to be ready to change your mind on, say, the role of optic tract in vision. Here is a quote from a paper by Galambos et al. (1967): "The visual capacities of eight cats following stereotaxic lesions that destroyed more than 85 per cent of their optic tracts were studied. Within a week post-operatively all of them resembled normal cats in most gross tests of visual abilities." Maybe the next book by Hickok could be "The Myth of Visual Pathways for Vision Perception".

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