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Do Mirror Neurons Subserve Action Understanding?

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Abstract

Mirror neurons were once widely believed to support action understanding via motor simulation of the observed actions. Recent evidence regarding the functional properties of mirror neurons in monkeys as well as much neuropsychological evidence in humans has shown that this is not the case

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Our understanding of the response properties of mirror neurons has been refined since they were first reported in the early 1990s. Specifically, we now know that mirror neurons are not mirroring specific motoric actions but rather something more abstract; something closer to the “goal” of the action. This has been demonstrated, for example, in the work of [24] who found that cells in F5 respond in a way that is aligned with the goal of a movement (to grasp food with pliers) rather than the specific movement itself (closing the hand with normal pliers vs. opening the hand with reverse pliers). What this observation highlights is that movements *per se* are ambiguous with respect to their meaning (the goals). If we observe a reaching movement towards a cup, the movement itself is ambiguous between several possible intentions: to take a drink, to hand the cup to someone, to move the cup out of the way, to clear the cup from the table, to reach just past the cup for something else, to throw the contents of the cup in someone’s face, and so on. To understand a movement, we need to understand the goal of the action.

This shifts the theoretical focus of investigation in that simulating a movement *per se* can’t be the mechanism for action understanding. Put differently, action understanding cannot be achieved by matching or simulating observed actions in one’s own motor system, as was once claimed, but by matching or simulating the *goals* of the actions. The question then becomes, how and where are the goals of an action coded in the brain?

Let’s consider the task employed by Umiltà et al., grasping food with pliers. What is the goal of such an action? As these authors suggest, there are both proximal and distal goals. Umiltà et al. suggest that the distal goal is to grasp the food (it is probably more accurate to describe this as an intermediate goal with the ultimate goal being something closer to eating the food, but let’s gloss over this), while the proximal goal is to grasp the pliers. The point of

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the Umiltà et al. study is to show that the distal goal at least is not a specific motor program, but rather a more abstract state. So what is it? How does the monkey know when he has achieved the intended goal? The answer is that the goal is encoded neurally as a sensory state: the visually determined positioning of the pliers around the food object and the somatosensory perceived change in resistance of the pliers. If the monkey were blindfolded and prevented from receiving somatosensory feedback, no matter how many movements he executed, accurately or not, the monkey would have no way to know whether the goal was achieved. The motor system alone is literally and figuratively blind and in this sense is incapable of understanding. The goals of an action are not in the actions themselves as Umiltà et al. have shown, they are in the *consequences* of the actions and these consequences are, for the range of actions we are considering here, sensory. Therefore, to understand an action, we must understand the *sensory* goal(s) of the action. Action understanding is a function of perceptual, not motor systems.

Having arrived at the conclusion that simulating actions does not itself determine action understanding (because movements are ambiguous and the targets or goals of movements are sensory), and with the discovery that mirror neurons don't seem to be selectively mirroring specific movements anyway [23], we are left with two questions. First, is there a sensory system that has the coding sophistication to analyze perceived actions and relate them to their sensory goals? And second, what are mirror neurons doing?

To address the first question, I'll quote from Rizzolatti and colleagues [22]:

The central point of the visual hypothesis is that a description of motor events in visual terms is sufficient for action understanding. The visual properties of some STSa [anterior superior temporal sulcus] neurons recently described by Perrett and coworkers [[13]] seem to support the visual hypothesis. Of particular relevance in this respect are neurons that combine information about the direction of gaze of an agent with the action performed by that agent. These neurons become active when the monkey sees the reaching action, but only if the action is performed with the agent's gaze directed to the intended target of reaching. So, if the agent performs an identical reaching action while looking away from the position to which the reach is directed, the neurons do not respond. It therefore seems that these higher-order visual neurons combine the output of neurons that are specifically responsive to the observation of arm reaching with the output of neurons that are specifically responsive to the direction of attention, as conveyed by the direction of gaze. Also, the behaviour of other STSa neurons, such as those that respond to goal-directed hand actions, can be taken as evidence in support of the visual hypothesis. (p. 665)

Cells in the STS seem to have all the right properties for supporting action understanding, that is, relating perceived actions with the sensory goals of the actions. Converging evidence is found in humans as well where the posterior STS has been identified as a site that is responsive to the perception of actions [6, 8]. Disrupting function in this region either via transcranial magnetic stimulation [7] or via degenerative brain disease [19] disrupts the perception of biological motion and/or action understanding, although the neuropsychological data remain equivocal [10, 20]. The point is that the mirror system isn't the only game in town when it comes to neural regions that are responsive to action perception.

The answer to the second question -- what are mirror neurons doing? -- is intensely debated. There are now at least three alternatives to the action understanding perspective. One is the sensory-motor association account proposed by Heyes and colleagues [2, 9] which argues that action execution and (self-)action perception co-occur and therefore become associated via sensory-motor learning in the response pattern of mirror neurons. A related alternative is

the action selection model, which holds that mirror neurons code relations between perceived actions and possible action responses on the part of the observer [11]. The idea is that (i) the action of others is relevant to one's own actions, (ii) there must be a neural mechanism for relating the perceived actions with appropriate response actions, and (iii) mirror neurons are highly likely candidate because they are found in a region (indeed system) that appears to perform just this function for object-action interaction (i.e., grasping objects). The action selection model, then, brings the mirror system into functional alignment with other dorsal stream action systems. The third account holds that mirror neurons are activated after an action is understood by other mechanisms as a means to make predictions about future actions [4]. One might at first view this kind of motor based predictive coding as simply the mechanism by which the mirror neurons enable action understanding, however, this would be incorrect. The evidence points to the conclusion that, as Csibra puts it, "[mirror neurons] *reflect* action understanding rather than contribute to it" (p. 443).

It is hard to distinguish the three accounts, in part because there has been little direct investigation aimed at teasing them apart. It is, however, relatively easy to rule out the action understanding account as it has been investigated extensively, particularly in the domain of speech, which is a function that mirror neurons were generalized to in the earliest publications [5, 21]. A straightforward prediction of the action understanding theory is that damage to the motor speech system should cause significant receptive speech deficits. This is not the case however. The ability to perceive speech sounds has been demonstrated in patients who have severely impaired speech production due to chronic stroke [18, 25], in individuals who have acute and complete deactivation of speech production due to left carotid artery injection of sodium amobarbital (Wada procedure) [12], in individuals who never acquired the ability to speak due to congenital disease or pre-lingual brain damage [1, 3, 15, 17], and even in nonhuman mammals (chinchilla) and birds (quail) [14, 16] which don't have the biological capacity to speak. These facts are flatly inconsistent with a motor theory of action understanding.

In summary, mirror neurons do not subserve action understanding.

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- Mirror neurons have been hypothesized to be the basis of action understanding
- Monkey evidence for this view is ambiguous
- Data from humans argues strongly against the action understanding claim
- There are now several alternative theories of mirror neuron function that don't reference action understanding