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Do mirror neurons really mirror and do they really code for action goals?

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Attempts to elucidate the properties of mirror neurons (MNs) have seen considerable effort expended and thousands of papers published. Nevertheless, the field is dogged by uncertainty and confusion: Not only is it harder than ever to say exactly what a MN is, but there is increasing ambiguity about their basic field properties and putative functions. Here we challenge the two properties of MNs which have excited most interest; that they 'mirror', and that they encode goals.

Do mirror neurons 'mirror'? It is frequently asserted that MNs respond selectively to the observation and execution of the same action (e.g., Arnstein et al., 2001; Chong et al., 2008; Dinstein et al., 2007, 2008), and thereby 'mirror' observed actions in the observer's motor system. For example, MNs are "visuomotor neurons that are active both during the execution of a movement and during the observation of the same movement" (Dinstein et al., 2007, p.1415). This description is typical, in that it implies that strict sensorimotor congruency - a close match between the effective actions during observation and execution - is a defining property of MNs. This definition accords with their unfortunate name, and in all likelihood, the intuition of many readers.

This intuition is, however, fundamentally inconsistent with the definition of MNs used by those responsible for their discovery ("[neurons] discharged when the monkey made active movements and when it observed specific meaningful actions made by the experimenter. We called these neurons mirror neurons"; Gallese et al., 1996, p.595). The practice of treating any unit responsive during action observation and execution as a MN, irrespective of sensorimotor congruency, continues to be routine in studies of their field properties.

So-called 'strictly congruent MNs', responsive to the *same* action during observation and execution, account for only 20-30% of MNs (e.g., di Pellegrino et al., 1992; Gallese et al., 1996). The majority of MNs are at best broadly congruent - responsive during the observation and execution of 'similar' actions (e.g., to the performance of grasping with the hand, but to the sight of grasping with the hand or mouth). These neurons clearly do not mirror the manner (i.e., effector, kinematics, trajectory) of action execution. The remaining MNs respond to the observation and execution of dissimilar actions (e.g., to the sight of food being placed on a surface, but the act of grasping food to eat) and have been termed logically-related MNs. The existence of suppression MNs - units that fire during action performance, but are inhibited during the observation of similar actions (e.g., Kraskov et al., 2009) – further complicates matters. Rather than 'mirror' observed actions, such units appear to systematically *prevent* mirroring.

Do mirror neurons encode goals? The view that MNs encode the 'goals' of observed actions, and thereby contribute to 'action understanding', is frequently presented as the prevailing consensus of the field (e.g., Fabbri-Destro and Rizzolatti, 2008). The term 'goal' is rarely defined explicitly but two definitions may be delineated. First, an action goal may refer to the object to which it is directed. Accordingly, many authors assert that MNs only respond to object-directed actions (e.g., "to be triggered by visual stimuli, mirror neurons require an interaction between a biological effector (hand or mouth) and an object"; Rizzolatti and Craighero, 2004, p.170). However, sufficient evidence exists to reject this view. As Rizzolatti and Craighero indicate, so-called 'mouth MNs' have been reported, responsive to the observation of lip-smacking and communicative actions performed in the absence of objects

(Ferrari et al., 2003). Moreover, examination of the early data reveals that 'pantomimed' actions (performed without objects) evoked responses in many MNs, albeit more weakly than object-directed actions (Gallese et al., 1996). Indeed, a more recent study found that 79% of MNs modulated their firing rate in response to pantomimed actions (Kraskov et al., 2009).

The second definition of 'goal' is as an effect on the world, or the intention behind an action (e.g., 'to grasp the peanut' or 'grasp the peanut to eat'). This suggestion was prompted by the observation that MNs "show a large degree of generalization. Presenting widely different visual stimuli, but which all represent the same action, is equally effective" (Rizzolatti and Craighero, 2004, p.170). The excitation of such high-level goal representations, when observing actions, is thought to help 'understand' those actions. For example, "only those [neurons] that can encode the goal of the motor behaviour of another individual with the greatest degree of generality can be considered to be crucial for action understanding" (Rizzolatti and Sinigaglia, 2010, p.269).

Crucially, however, the overwhelming majority of MNs *are* sensitive to low-level features of observed actions that alter their visual appearance but not their goal. For example, Gallese et al (1996) reported that the firing of 38% of MNs depended on whether right- or left-hand actions were observed, while 64% were sensitive to the direction (i.e., right-to-left or left-to-right) of the same reaching action. Similarly, MN firing typically depends on whether the observer monkey can reach the target object (53% of MNs; Caggiano et al., 2009) and the observer monkey's viewpoint (73% of MNs; Caggiano et al., 2011). If MNs encoded goals, whether goals are objects or intentions, their responses should be invariant to these features. The goal of an observed movement (e.g., 'grasp the peanut to eat') is the same irrespective of

which hand is used, the direction of reaching, whether the observer can reach the target-object, or the observer's viewpoint. Very few MNs therefore have field properties consistent with the goal-coding hypothesis. Indeed, variable MN sensitivity to low-level information highlights the need to examine responses at a population level.

Conclusion. The pace with which the MN literature continues to expand is both a blessing and curse. Whilst novel datasets promise compelling new insights, there is growing inconsistency and tension in the fundamental assumptions, made by different authors, about the defining properties of MNs. It is more important than ever that researchers read closely the original descriptions of the field properties of MNs, and do not rely on (necessarily) simplified accounts presented in review articles.

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