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Positions in the Mirror Are Closer Than They Appear

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Abstract

When contributions to the Mirror Neuron Forum (Gallese, Gernsbacher, Heyes, Hickock, & Iacoboni, 2011, this issue) are viewed optimistically, it is clear that progress is being made in understanding whether and how the human mirror neuron system supports psychological processes as diverse as action understanding, speech perception, and social cognition. Nonetheless, further progress requires not just more data, but also theoretical and methodological advances.

Keywords

mirror neurons, neuroscience, cognition

At lunch with Leo Fogassi several years ago, I remarked on the danger of everyone in the University of Parma's Neuroscience Department working on mirror neurons (MNs). "What if you're wrong?" His reply was that the data were overwhelming, "I am sure about the validity of our observations." I agree with Leo: The evidence that MNs in the macaque discharge both during action execution and action observations is, for the most part, unchallenged. Similarly, we are almost to the point that there is no question regarding the existence of MNs in humans (e.g., Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010). But as the answers and replies in the Forum (Gallese, Gernsbacher, Heyes, Hickock, & Iacoboni, 2011, this issue) reveal, there is hardly unanimity regarding other data and the interpretation of those data.

So, where do we stand? The research is hampered both by fallible methods (as reviewed in the Introduction) and lack of theoretical precision. Nonetheless, my admittedly biased and optimistic analysis of the Forum suggests that progress is being made, and even the most contentious interchanges suggest directions for future work.

Question 1: Do Mirror Neurons in Macaques or Humans Make an Important Contribution to Action Understanding?

The wide-ranging discussion engendered by this question touched on issues of action selection and action understanding, as well as differences between imitation and observation.

Gernsbacher (Q1 reply) notes that the data are squarely contrary to one prediction she attributes to MN theory: The fMRI bold signal in the MN system should be larger during imitation of well-known actions than during imitation of novel actions. But is this a generally accepted prediction? Certainly the theories predict a greater fMRI signal for observation of well-known versus novel actions, but as Iacoboni (Q3-answer) notes, learning to imitate novel actions is more complex. Here is a clear case where theoretical precision is needed: What are the predictions for the MN system while learning to imitate?

There is greater agreement that an MN system plays some role in action processing, but as Gallese (Q1 answer) writes, "... it is fair to say that action understanding, even at a basic level, does not necessarily require the activation of [MNs]," that is, other mechanisms also can play a role, and this will make theory testing difficult. Furthermore, to the extent that an MN system does influence action processing, is that influence the priming of actions for future selection (Hickok, Q1 answer) or something like understanding from "within" (Iacoboni, Q1 answer)? Iacoboni suggests that one component of understanding from within is enhanced prediction, but Hickok takes prediction to be a measure of

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selection not action understanding. And so we come to Heyes's (Q1 reply) point: "So what is the dispute really about? My guess is that it concerns, not what *causes* action understanding, but what *constitutes* action understanding," (emphases added). Certainly understanding the goal of an action would seem to be central to what is meant by action understanding, but Hickok (Q1 reply) asserts that goals are cognitive and outside the motor system. In contrast, Gallese (Q1 answer) takes the representation of action goals to be among the central functions of MNs. My conclusion is that a theory of goals and their neural, cognitive, and bodily instantiation will be needed before Question 1 can be given a satisfactory answer.

Question 2: Do Mirror Mechanisms Causally Contribute to Speech Perception and Language Comprehension?

Gernsbacher, Gallese, Hickok, and Iacoboni agree that the motor system has some role in speech perception, but there is disagreement as to whether that role is major or small, modulatory, and inconsistent. Gernsbacher (Q2 reply) observes that effects supporting an MN system tend to occur when speech is embedded in noise, responding is slow, and consequently atypical strategies might be engendered by the experimental situation. However, a positive spin on Gernsbacher's observation is that contributions from an MN system may be most evident when listening to speech in less than ideal situations—situations that may well be representative of natural conversation outside of the laboratory.

An interesting convergence revolves around the notion of corollary discharge. Some theories of motor control (e.g., Wolpert & Kawato, 1998) propose that a copy of motor commands (i.e., a corollary discharge) is used by predictor models to generate predictions of the sensory consequences of the motor activity. Hickok (Q2 answer) has incorporated this position into a model of speech perception, and he proposes that the motor system modulates speech perception through such a mechanism. Note the similarity of this idea to Iacoboni's (Q2 answer) position that "Mirror mechanisms may implement top-down motor-based models of the acoustic input." Finally, the notion of corollary discharge leading to prediction is central to a model of language production and comprehension (Glenberg & Gallese, 2011) in which MNs play a role in the predictor models. Thus, developing a better understanding of the role of motor-based prediction in speech and language comprehension will undoubtedly help to answer Question 2.

Question 3: Do Mirror Mechanisms Contribute to Imitation?

Gernsbacher's (Q3 answer) historical analysis documents misinterpretations of some of the early work on MNs and imitation. As reviewed by Gallese (Q3 answer, Q3 reply), Heyes (Q3 answer, Q3 reply), and Iacoboni (Q3 answer, Q3 reply), the more recent literature is methodologically more sound and internally consistent. As Heyes writes, when

imitation is defined in terms of action topography, the data support a causal role for an MN system in imitation.

Question 4: Do Mirror Neurons Get Their Characteristic Visual-Motor Matching Properties From Learning?

Gallese (Q4 answer), Heyes (Q4 answer), and Iacoboni (Q4 answer) agree that MN activity can be changed by experience. Nonetheless, there are at least two issues that need to be resolved. The first is whether MNs are anything special, or as Heyes (Q4 answer) proposes, MNs are motor neurons that have had the opportunity to associate visual and motor inputs. An alternative, at least in regard to the initial development of MNs, is Gallese's (Q4 answer) hypothesis that motor activity (even in utero) can tune visual areas for inputs that match the spatio-temporal characteristics of the motor activity. A related issue is the degree to which neonatal imitation is a reliable phenomenon (see Heyes, Q4 reply) because if it is not, then there is less of need for a hypothesis such as Gallese's. The second issue is whether and how a neuron that develops associations between visual and motor inputs works to causally effect processing (a need for theory, again).

Question 5: To What Extent Does Variability in Mirror Mechanism Functioning Contribute to the Autistic Phenotype?

Even within this most contentious area, there is some hope of moving forward. First, all agree that autism is a complex syndrome that is unlikely to have a simple explanation: Even if MNs play a role in autistic behavior, they will certainly be only part of the story. Second, as the data (inconsistencies and all) start to eliminate simple hypotheses, they open the field for more complex and nuanced accounts of the possible role of an MN system in autism.

As one example, consider Iacoboni's (Q5 reply) suggestion for how downregulation of the gene *RORA* in males can affect development of the cerebellum, which in turn could affect development of BA 44 (part of Broca's area and the MN system). As another example, both Gallese (Q5 answer) and Gernsbacher (Q5 reply) cite a paper by Boria et al. (2009) that documents conflicts in the literature and attempts a resolution based on two distinctions. The first distinction is that action understanding involves an answer to a "what" question (e.g., What is that person doing? Grasping a cup) and a "why" question (e.g., Why is that person grasping the cup? To take a drink or to clean up?). The second distinction concerns the information used in answering the why question: Is the information motoric (e.g., hand shape and kinematics) or contextual (e.g., the cup is empty or full)? Boria et al., propose that the MN system is particularly important in answering the why question in the absence of strong contextual information. In fact, Boria et al.'s data show that high-functioning autistic children

are equal to the typically developing children in many action-understanding tasks. However, when answering the why question on the basis of motor behavior with limited contextual information, the autistic children show a selective deficit. Thus, this enhanced (and nuanced) theoretical precision regarding the nature of action understanding and contributions of the MN system to action understanding may help to resolve some of the contentious issues and claims regarding the role of an MN system in autism.

Question 6: To What Extent Do Mirror Mechanisms Contribute to Social Cognition Such as Similarity Bias, Empathy, and Cultural Transmission?

As in a fairy tale, we end with unanimity—at least on the surface. As Heyes (Q6 reply) notes, “The answers to Question 6, and to Questions 1–3 and 5, confirm that authoritative figures in the field believe that MNs play a fundamental role in a range of social cognitive functions.” Going further, Iacoboni (Q6 answer) writes, “Thus, neural mirroring in humans potentially represents a bio-marker of sociality,” and Gallese (Q6 answer) suggests that “mirroring could be a basic functional principle of our brain . . .” Still, as Iacoboni (Q6 answer) notes, there are “conflicting findings.” In addition, we are far from having a definitive analysis of how MNs play a role in social/cultural processes, and as Heyes (Q6 answer) observes, we need to understand the reverse: how cultural processes help to shape MNs. Nonetheless, it is perhaps not too early to be as optimistic as Heyes (Q6 reply) when she suggests that, “if plausibility arguments give way to solid evidence that MNs have

major effects on social cognition . . . [that] would indicate the power, not only of MNs, but of the associative learning and sociocultural processes that put them in our brains.”

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