Discussion forum

A new approach to mirror neurons: Developmental history, system-level theory and intervention experiments

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The standard view of mirror neurons (MNs) or 'genetic account' alloys a claim about the origin of MNs with a claim about their function (e.g., Rizzolatti & Craighero, 2004; Rochat et al., 2010). It suggests that the mirrorness of MNs − their capacity to fire during the observation and execution of similar actions − is due in large measure to heritable genetic factors, and that the genetic predisposition to develop MNs evolved because MNs facilitate action understanding. This account casts MNs as 'an adaptation' (Williams, 1966) for action understanding; it suggests not merely that MNs *can do* action understanding, but that they were designed by evolution *for* action understanding. In contrast, the 'associative account' separates questions about the origin and function of MNs (e.g., Heyes, 2010). It proposes that MNs acquire their capacity to match observed with executed actions through domain-general processes of sensorimotor associative learning (Fig. 1). In evolutionary terms, MNs are not *for* anything, and whether they *can do* action understanding, or any other social cognitive function, is an open empirical question.

In a recent, comprehensive review, my collaborators and I argued that the balance of evidence now favors the associative account over not only the genetic account, but also hybrid models proposing that MNs develop through associative learning and constitute an adaptation for action understanding (Catmur, Press, Cook, Bird, & Heyes, 2013; Cook, Bird, Catmur, Press, & Heyes, 2013). Specifically, we argued that 1) mirror neurons do not consistently encode action 'goals'; 2) the contingency- and context-sensitive nature of associative learning explains the full range of mirror neuron properties; 3) human infants receive enough sensorimotor experience to support associative learning of mirror neurons; and 4) mirror neurons can be changed in radical ways by sensorimotor

training (e.g., Catmur, Mars, Rushworth, & Heyes, 2011; Cavallo, Becchio, Heyes, & Catmur C, 2013; Cook, Dickinson, & Heyes, 2012; Landmann, Landi, Grafton, & Della-Maggiore, 2011; Press, Gillmeister, & Heyes, 2007; Press, Catmur, Widman, Heyes, & Bird G, 2012)

The genetic account was inspired by a distinctive method of investigating the function MNs. This method focuses on the field properties of MNs found in a sample of laboratory monkeys with unreported developmental histories. It asks, usually without reference to pre-existing computational or psychological theory, what neurons with these field properties would be 'good for', what they might have been designed by evolution to do. The associative account suggests that this approach needs to be changed and extended in three principal ways:

1. Developmental history

If MNs were a genetic adaptation, it is likely that their properties would be relatively invariant across developmental environments. Consequently, it would be possible to make valid inferences about species-typical properties of MNs based on a relatively small and developmentally atypical sample of individuals. If MNs are instead a product of associative learning, this kind of inference is not valid. Whether or not an individual has MNs, which actions are encoded by their MNs, and at what level of abstraction, will all depend on the types of sensorimotor experience received by the individual in the course of their development. Therefore, the associative account implies that it is crucial for studies of laboratory monkeys to report, and ideally to control, the animals' developmental history, the kinds of sensorimotor experience

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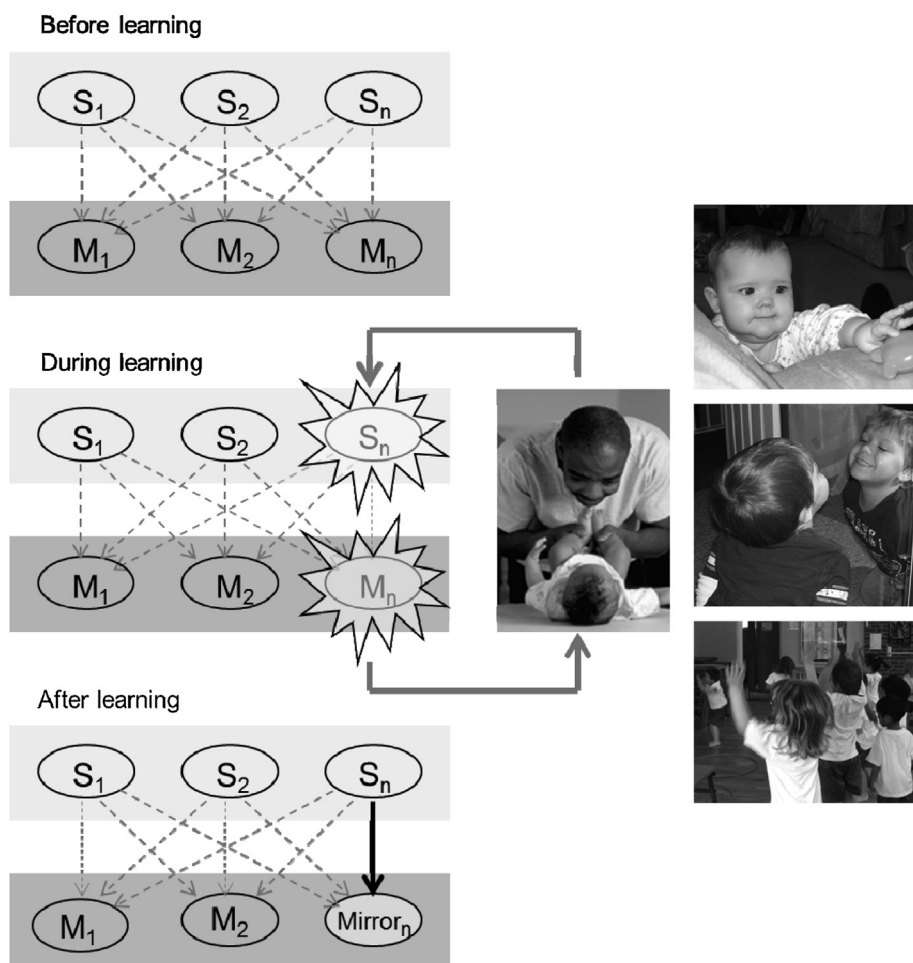E-mail address: cecilia.heyes@all-souls.ox.ac.uk.

Fig. 1 – The associative, or 'Associative Sequence Learning' (ASL), account of the origin of mirror neurons (reprinted with permission from Heyes, 2010). Before learning, sensory neurons in STS (S_1, S_2, S_n), encoding visual descriptions of observed action, are not systematically connected to motor neurons in premotor and parietal areas involved in the production of similar actions (M_1, M_2, M_n). Learning occurs when there is correlated activation of sensory neurons (e.g., Sn) and motor neurons (e.g., Mn) coding similar actions – e.g., during self-observation, during synchronous social activity or when an adult imitates an infant. Correlated (contiguous and contingent) activation of Sn and Mn increases the strength of the connection between them, so that activation of Sn is propagated to Mn. Therefore, after learning, Mn is a mirror neuron.

to which they have been exposed. It also suggests that, if we want to know the species-typical properties of monkey MNs, it will be necessary to test monkeys that have received all and only the types of sensorimotor experience typically available to them under free-living conditions.

2. System-level theory

If MNs were a genetic adaptation, one could argue that new categories of psychological functioning – such as 'action understanding', 'motor resonance' and 'embodied simulation' – are necessary to characterize what they do. It could be argued that, since they were specifically favored by natural selection, MNs are likely to have a distinctive, independent, and previously unrecognized psychological function. In contrast, by showing that established psychological theory – associative

learning theory – can cast light on the origin of MNs, the associative account underlines the value of embedding research on MN function within system-level psychological and computational theories of how the brain produces behavior (e.g., Giese & Poggio, 2003). A system-level approach implies that, whatever their origins, hypotheses about MN function should specify a part in a process – a process that goes all the way from peripheral sensory input to overt motor output – that MNs are thought to fulfill (Heyes, under review). The name assigned to this part is not important in itself. What is important is that the hypothetical function of MNs is distinguished clearly from other components of the same overall process. For example, 'action understanding' needs to be distinguished in an empirically testable way from 'action perception', 'action recognition', 'action selection' and 'mentalising' (Gallese, Gernsbacher, Hickok, Heyes, & Iacoboni, 2011).

3. Intervention experiments

Human research on MN function faces a formidable localization problem. Single-unit recording is seldom possible with human subjects, and therefore most studies assume that activity in ventral premotor cortex and the inferior parietal lobule is MN activity. This is unsatisfactory because monkey data suggest that fewer than 20% of the neurons in these areas are actually MNs. Given this problem, it would be valuable to conduct animal studies that, not only record the field properties of MNs, but also examine how those properties relate to behavioral competence. For example, are animals with MNs for actions X and Y better than other animals of the same species at behavioral discrimination of X and Y, or at imitating X and Y? Studies of this kind have been dismissed as impractical on the assumption that they would have to involve monkeys, and that between-group variation in MN activity would have to be induced via invasive procedures. However, the associative account suggests that it may be possible to overcome these problems by establishing a rodent model, and using sensorimotor training to induce between-group variation in the number and type of MNs present in rodent (and monkey) brains.

The associative hypothesis is functionally permissive. It suggests that MNs were not shaped by evolution to fulfill any specific function, but allows that they could contribute to social cognition in a variety of ways. It encourages us to ask not what MNs are *for*, but what they *can do*, and tells us how to search for the answers.

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