Many questions about contagious behavior and MNs remain. Building on the above results for contagious yawning and itching/scratching, should we conclude that the sufficiency of a variety of multimodal stimulus triggers is evidence against the behavioral involvement of MNs, instances of broadly tuned or multiple MNs, or examples of a different class of mirror-like acts that do not involve MNs? Do environmental contingencies influence the tuning of stimulus triggers or MNs, possibly contributing to the acquisition of multimodality? And what about other contagious behaviors? To what extent does the contagiousness of nausea/vomiting, coughing (but not sneezing), vocal crying, laughing, and yawning involve shared feeling states or another, more specific trigger (Provine 2012)? The answers to these questions may come from developmental, comparative, and perceptual studies that are now underway. Whatever the outcome, such research will broaden our understanding of the neurological basis of sociality.

Experiential effects on mirror systems and social learning: Implications for social intelligence

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Abstract: Investigations of biases and experiential effects on social learning of social information use, and mirror systems can usefully inform one another. Unconstrained learning is predicted to shape mirror systems when the optimal response to an observed act varies, but constraints may emerge when immediate error-free responses are required and evolutionary or developmental history reliably predicts the optimal response. Given the power of associative learning, such constraints may be rare.

Cook et al. present a compelling case that mirror neurons (MN) have a developmental origin in associative learning. Moreover, they legitimately argue that empirical testing is required to determine whether MNs and mirror systems have evolutionary origins as adaptive specializations, echoing criticism of adaptationist “just-so” stories in other fields (Pigliucci & Kaplan 2000). Here, I discuss whether work on mirror systems can be informed by, and inform, the fields of social information use and social learning. I leave aside discussion of communicative signals, by definition adaptive specializations.

Many animals use social information (information provided by other individuals) and social learning (learning from this information) as adaptive specializations, echoing criticism of adaptationist “just-so” stories in other fields (Pigliucci & Kaplan 2000). Here, I discuss whether work on mirror systems can be informed by, and inform, the fields of social information use and social learning. I leave aside discussion of communicative signals, by definition adaptive specializations.

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social learning, rather like predispositions to attend to conspecifics protect young birds from errors during filial imprinting (Horn 2004).

Given that predispositions are expected for certain forms of social information use, the unconstrained flexibility of mirror systems that Cook et al. note raises two possibilities, assuming that mirror system efficiency is a determinant of fitness. Either (1) mirror system flexibility is vital to their adaptive function, suggesting that social cues have variable meanings that must be learned, or (2) evolved alternatives to associatively acquired mirror systems are constrained, perhaps by their cost. The broad affordances of associative learning may mean that beneficial mirror systems come virtually “for free,” reducing the likelihood of alternate evolved solutions.

If mirror systems and social learning tendencies are the products of general learning processes, the evolution of social and general intelligence may be closely entwined (Brown & Brüne 2004). Furthermore, because associative learning and social information use are phylogenetically widespread, mirror systems could be studied in species such as insects, where evolutionary studies could examine the related but separate questions of adaptiveness and associative specialization. Particularly informative would be studies of species where deviating from group behavior carries strong costs, such as certain fish (Bates & Chappell 2002). Studies of links between mirror system efficacy and behavioral competence are essential, ideally by measuring costs and benefits for fitness in “real-world” group situations to establish when individuals out-compete or interact more effectively with others. Cook et al. present a parsimonious model that inspires broad application and testing of mirror system concepts.

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Confounding the origin and function of mirror neurons
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Abstract: Cook et al. argue that mirror neurons originate in sensorimotor associative learning and that their function is determined by their origin. Both these claims are hard to accept. It is here suggested that a major role in the origin of the mirror mechanism is played by top-down connections rather than by associative learning.

The characterizing feature of the primary visual cortex of primates is the presence of neurons sensitive to stimulus orientation. Regardless of whether the orientation-sensitive neurons are determined genetically or acquired by experience, or both, they are at the basis of the functional organization of primates’ visual system (Hubel & Wiesel 1998; Marr 1982). The same is true for mirror neurons (MNs). Regardless of whether their properties are determined genetically, acquired by experience, or both, they represent the neural substrate of a fundamental mechanism that transforms sensory information into a motor format (the mirror mechanism).

The functions of the mirror mechanism vary from action understanding, to imitation, to empathy, and even, in birds, to song recognition (Rizzolatti & Sinigaglia 2010). Their function depends on their anatomical location. Thus, contrary to the view advanced in the present target article, the problem of how MNs originate is utterly irrelevant as far as their function is concerned. It is an interesting problem, but it has little to do with the function of the mirror mechanism.

The claim that mirror neurons are just “another type” of association neurons misses their characterizing, unique property, which is that of giving a motor format to sensory stimuli. This misunderstanding can be also found in an interesting paper on mirror neurons by Damasio and Meyer (2008). They claimed that the parieto-frontal mirror neurons are new neural ensembles included in higher-order association areas called “non-local convergence-divergence zones” that collect information from lower-order visual, auditory, and somatosensory association areas, and signal back to those areas. Action understanding depends on the activation of this network. This proposal had the merit of highlighting the role of top-down connections in action understanding. It overlooked, however, as done in the present target article, the fact that parieto-frontal mirror neurons are motor neurons. When MNs discharge, they “ignite” motor schemata similar to those endogenously activated during motor imagery and, within limits, during actual motor act execution. In other words, my motor schemata are activated during the observation of similar motor schemata of others. This provides a neurophysiological account of the mechanism underlying action understanding “from inside” (Rizzolatti & Sinigaglia 2010); a first-person process, where the self feels like an actor, rather than a spectator (Jeannerod 1997, p. 95; emphasis added). This appears to be a function that only the mirror mechanism is able to mediate.

Mirror neurons have top-down effects (Damasio & Meyer 2008, see also Kilner et al. 2007b). In other words, following MN activation, signals go not only toward other motor areas, but also backwards to lower-order visual, auditory, and somatosensory areas. This top-down activation binds the understanding of what a person is doing (e.g., grasping), encoded in the motor cortex, with the visual details of that action. An interesting possibility is that the top-down mechanism also has another function, which is: to be the neural substrate of a learning mechanism that starts from motor centers rather than from the environment. An elegant experiment by Van Elk et al. (2008) illustrates this point well. EEG was recorded during observation of action videos in 14- to 16-month old infants. Desynchronization of the movements-related rhythms (e.g., mu rhythms) was found for the observation of crawling, but not for the observation of walking. Furthermore, the size of the effect was strongly related to the infant’s own crawling experience. The authors concluded that experience of one’s own actions is closely related to how actions of others are perceived.

Cook et al. dismiss the experiments showing that human neonates are able to copy actions done by others (Meltzoff & Moore 1977). Their argument is the following. The best-documented imitative action is tongue protrusion, but even this act “lacks the specificity … of imitation” (target article, sect. 6.1, para. 1). In addition, this behavior can also be elicited when infants observe a mechanical “tongue” or disembodied mouth. It is hard for me to conceive how the mirror mechanism of a neonate might have a neurological maturity such as to provide a precise copy of tongue protrusion. Occasionally this could happen, but the potential act encoded in a newborn must be, for maturational reasons, just “protruding.” Note also that grasping MNs generalize across the observed actions having the same goal. For example, in both monkeys and humans the observation of a grasping robot arm is effective in triggering mirror neurons (Gazzola et al. 2007, Peeters et al. 2009; Rochat et al. 2010), exactly as does the “mechanical tongue” in the example mentioned above. My hypothesis is that tongue protrusion in newborns is an effect mediated by a mirror mechanism similar to that described for crawling by Van Elk et al. (2008). Action comes first and links motor centers with sensory centers. Once these connections are established (or reinforced), the external information can flow in a forward direction, from stimuli to actions. Hence the imitation.