

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, 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 (MNs) 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; Reader & Biro 2010). Debate over mirror system origin and function can be viewed as part of a broader debate over the origins of a reliance on social cues and of the mechanisms underlying social information use, a debate Heyes (1994; 2012a; 2012c) has also championed. Besides the fact that mirror systems utilize social information, there are numerous points of intersection between the two research fields. Mirror systems have been proposed to underlie various forms of social learning, including stimulus enhancement, emulation, and imitation learning (Byrne 2002; Keyesers & Perrett 2004), and such systems could potentially associate personal and conspecific location and thus also underlie local enhancement. Social learning propensities, biases, and processes have been proposed to be products of general learning processes, in a similar fashion to the Cook et al. proposal (Church 1957; Heyes 1994; 2012c; Keyesers & Perrett 2004; Laland & Bateson 2001; Leadbeater & Chittka 2007; Miller & Dollard

1941). Furthermore, like mirror systems, the assumption that social learning is an adaptive specialization has been questioned, as has whether any such adaptive specialization would involve input systems rather than the learning mechanisms themselves (Caldwell & Whiten 2002; Heyes 2012c; Lefebvre & Giraldeau 1996; Reader et al. 2011). These points of intersection suggest the two fields may usefully inform each other.

Experiential effects on the propensity to use and learn from social information have been demonstrated in several species (Kendal et al. 2009), supporting the idea that responses to social cues can be learned. However, flexibility alone is insufficient to demonstrate that the value and meaning of social cues are acquired by learning, since flexibility could be genetically encoded. For example, individuals could follow evolved unlearned rules-of-thumb of when, where, and how to employ social information (Rendell et al. 2011). Direct manipulation of the benefits of social information provides superior evidence for learned biases in social information use. For example, sparrows raised with an artificial parent that had reliably indicated food were more likely to approach feeding conspecifics than if the parent had not reliably indicated food (Katsnelson et al. 2008). Similarly, in finches manipulation of the net benefits of attending to others resulted in changes in individual tendencies to use social information, with lags that suggested the birds were learning the optimal response on the basis of received rewards (Mottley & Giraldeau 2000). Perhaps the most compelling current evidence for associative learning shaping social information use involves the acquisition of matching and nonmatching responses during social learning. Dawson et al. (2013) trained bumblebees in a feeding array where conspecific “demonstrators” indicated either the presence of sweet sucrose or bitter quinine. Bees thus readily learned to approach or avoid conspecifics. Later, the bees observed demonstrators at one color of flower in a two-color array. Bees previously rewarded for approaching conspecifics were more likely to choose the same color as demonstrators, whereas the reverse was true in the quinine-trained bees. Such data strikingly parallel mirror and counter-mirror effects observed in budgerigars and dogs (Mui et al. 2008; Range et al. 2011).

Although these examples provide evidence that experience can shape reliance on social cues, interpreting all individual and between-species variation in social information use as the result of prior learning would risk telling *associationist* “just-so” stories. Studies of the evolution of learning provide useful insights into when an evolutionary account may explain variation in social information use (e.g., Boyd & Richerson 1985; Dunlap & Stephens 2009; Johnston 1982). When opportunities for learning are limited, learning or errors are costly, or the optimal response to a social cue is highly predictable, natural selection could shape genetically encoded predispositions to respond in a certain manner to particular social cues. Similarly, if experiences in early life predict later payoffs of social information, and there are costs to learning, early life experience may result in fixed social learning tendencies during adulthood (Lindeyer et al. 2013).

There are several instances where responses to social cues appear fixed. Cases such as humans copying the most successful individual even when this is suboptimal (Offerman & Schotter 2009), birds ignoring reliable asocial information to copy conspecifics (Rieucou & Giraldeau 2009), and the aforementioned counter-mirror effects taking longer to develop than mirror effects could all be the result of the extensive social experience individuals have prior to testing. However, other examples are more difficult to explain in terms of experiential effects. For example, several avian species use conspecific and heterospecific nesting or breeding success during their own habitat selection without clear opportunities to learn to use these cues (although experience can shape later choices; Morand-Ferron et al. 2010). Restrictions on the stimuli monkeys and warblers socially learn about are also consistent with an adaptive specialization account (Davies & Welbergen 2009; Mineka & Cook 1988, but see Heyes 1994). Such predispositions would reduce errors during

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 2012; Dunbar & Shultz 2007; Reader et al. 2011). 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 adaptive 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 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.