

enables intended movements (goal-directed acts) to be prescribed by predictions, which action is enslaved to fulfill. In this framework, the “mirroredness” of MNs simply reflects the fact that the content of the representations, the action, remains the same in action execution and observation. What changes is the context, or agency—whether the action was produced by the self or another. Therefore, whatever account, genetic or associative, best explains the ontogeny of mirror neurons, it must hold for both action observation and action execution. Within the active inference framework, any selective pressure must operate at the level of agency (self or other) and not at the level of the mirror neurons.

Cook et al.’s article highlights the important point that it is incredibly hard to disambiguate the genetic and associative contributions to the ontogeny of a specific neuronal population. This is because all neurons show associative plasticity, and their response profiles can be modified through interactions with the environment—where these modifications depend upon heritable (genetic) synaptic (associative) plasticity. For example, orientation-tuned responses in neurons in primary visual cortex can be elicited in kittens as soon as they open their eyes—suggesting that the orientation maps are innate. However, depending on the environment, the orientation-tuning can be optimised during development to reflect the observed world (Blakemore & Mitchell 1973). If a kitten is raised in an environment with only vertical stripes, the response properties of the kitten’s neurons in the primary visual cortex will reflect this and responses to horizontal stimuli will be lost. In addition to this, many responses of neuronal populations that we think of as being a result of evolutionary adaptations—for example, binocular disparity responses and direct cortico-motoneuronal cells—are not present at birth but develop postnatally. This is in distinction to the formal phenotypes that contextualise the function of these neurons; for example, having two eyes and opposable thumbs. Indeed, for visual responses, the consensus view is that the primary repertoire of connections that underlie vision are present at birth and are fundamentally refined by early postnatal experience. In other words, it is not the neurons that are the genetic adaptation, but rather, how they form connections. In this light, it is tempting to propose the same for the visuomotor responses of MNs. In other words, mirror neurons arise as a result of domain-general mechanisms of associative learning, as proposed by Cook et al., but in the context of cortical connections between visual and motor systems selected by genetic adaptation. From this point of view, with respect to the ontogeny of MNs, perhaps we should consider that no neuron is an island?

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A developmental perspective on action and social cognition

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Abstract: The target article argues that developmental processes are key to understanding the mirror neuron system, yet neglects several bodies of developmental research that are informative for doing so. Infants’ actions and action understanding are structured by goals, and the former lends structure to the latter. Evaluating the origins and functions of mirror

neurons depends on integrating investigations of neural, social-cognitive and motor development.

Cook et al. articulate two conclusions with which we wholeheartedly agree: (1) The functions of mirror neurons (MNs) cannot be determined based only on patterns of neural activation during action observation. Independent measures of the putative social-cognitive functions of MNs are needed and have, so far, not been sufficiently integrated with neural measures; and (2) understanding the developmental origins of MNs and the broader systems in which they are situated is essential for understanding their functional significance.

Given the centrality of developmental processes to Cook et al.’s arguments, we find it surprising that they do not engage the developmental literature more fully. They propose a relatively simple learning process—the formation of contingency-based associations between visual and motor experience—to account for the existence of MNs. For example, they propose that MNs reflect repeated experiences with reaching for objects and seeing the resulting hand movements. This kind of learning seems very likely to occur, but without a fuller consideration of motor and social-cognitive development, it is difficult to see how any important social-cognitive functions could arise from motor experience. In fact, several bodies of experimental work with human infants indicate that much richer connections exist between motor experience and social cognition.

Developmental research shows that infants’ actions are prospectively goal-directed from very early in infancy (von Hofsten 1980; 2004), and during the first year, manual skills become increasingly well-organized (Thelen et al. 1996; von Hofsten & Ronqvist 1988). For example, Claxton et al. (2003) demonstrated that infants reach for objects differently depending on what they intend on doing next: They are faster to reach for a ball if they are going to throw it versus place it into a container. Further, over the course of the first year of life, infants begin to systematically anticipate the shape, size, and orientation of the objects that they grasp (von Hofsten & Ronqvist 1988). This body of work shows that motor competence even in young infants involves abstract action plans, as it does in adults (Rosenbaum 1991). This fact about infants’ actions has implications for the role that action experience might play in infants’ perception of others’ actions as organized by goals.

In fact, converging research has shown that infants also view others’ actions as structured by goals. Infants encode others’ actions in terms of the relation between agent and goal (e.g., Brandone & Wellman 2009; Luo & Johnson 2009; Sodian & Thoermer 2004; Sommerville & Woodward 2005; Woodward 1998), selectively imitate the goals of others’ actions (Gerson & Woodward 2012; Hamlin et al. 2008; Meltzoff 1995), and anticipate the outcomes of others’ actions based on their goals (Cannon & Woodward 2012; Gredebäck et al. 2009; Kanakogi & Itakura 2010; Krogh-Jespersen & Woodward, under review). Moreover, across these findings, matched comparison conditions and fine-grained analyses of infants’ attention during the tasks have shown that infants’ responses reflect more than simply attention to physical movements or low-level associations between hands and objects. Instead, this body of evidence shows that infants analyze others’ behavior in terms of the abstract relational structure that organizes goal-directed actions.

Importantly, infants’ action understanding is related to and shaped by their action experience. The emergence of goal-directed actions in infants’ own motor repertoires correlates with their analysis of these actions in others (e.g., Brune & Woodward 2007; Cannon et al. 2012; Kanakogi & Itakura 2011; Loueks & Sommerville 2012; Sommerville & Woodward 2005). Critically, interventions that change infants’ own actions render changes in their analysis of others’ action goals. For example, 3-month-old infants are not yet efficient at reaching, but, given training to use Velcro “sticky” mittens to apprehend objects, they subsequently demonstrate an understanding of others’ reaches as

goal-directed (Sommerville et al. 2005). Matched training that involves passively observing others' reaches does not have this effect (Gerson & Woodward 2014; for related findings, see Libertus & Needham 2010; Sommerville et al. 2008). Thus, this body of work shows that infants' own experience producing goal-directed actions informs their understanding of the goals that structure others' actions.

Nevertheless, studies of infants have made only preliminary progress in the domain in which the MN hypothesis originated – neural processes. We agree with Cook and colleagues that a systems approach is needed to evaluate the functional relations that may be signaled by the firing properties of MNs. In human infant research, we have neither the precision of single-cell recordings nor (yet) an analysis of connectivity among potential components of the mirror neuron system (MNS). Even so, infants evidence neural activity in the motor system during observation of others' actions (Marshall et al. 2011; Nyström et al. 2011; Southgate et al. 2009). Critically, changes in infants' motor experience modulate this neural response to others' actions. Developments in infants' motor skill affect the motor system's response to others' actions (Cannon et al., under review; van Elk et al. 2008), and short-term manipulations of motor experience in infants generate similar effects (Marshall et al. 2013; Paulus et al. 2012). Yet, as Cook et al. point out with regard to the adult work, the critical connection between the MNS and social understanding has not been made for infants. Establishing this connection requires integrating neural techniques with behavioral methods for investigating social cognition in infants.

Cook et al. use a developmental framework to argue against over-interpretation of MN findings. While we see merit in their argument that many open questions still exist concerning the MNS, we also advise against throwing out the baby with the bathwater. Rather than using developmental arguments to minimize the potential significance of MNs for social cognition, the field should be pushing forward to understand the links between neural systems, social cognition, and motor skill. Because each of these systems undergoes rapid and dramatic change during early ontogeny, a developmental approach is likely to shed the most light on the links between them.

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The origin and function of mirror neurons: The missing link

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Abstract: We argue, by analogy to the neural organization of the object recognition system, that demonstration of modulation of mirror neurons by associative learning does not imply absence of genetic adaptation. Innate connectivity defines the types of processes mirror neurons can participate in while allowing for extensive local plasticity. However, the proper function of these neurons remains to be worked out.

The article by Cook et al. addresses the question whether mirror neurons (MNs) are a genetic adaptation for action understanding. The authors argue that if this were the case, one might predict that

their functioning would be protected against “environmental perturbations” (sect. 7.1, para. 1). They make the further claim that if it could be demonstrated that the functioning of MNs can be modulated by associative learning, such an outcome could be taken as evidence against the genetic adaptation hypothesis.

One may question the prediction that if mirror neurons were “designed by evolution” for action understanding, their response properties should likely be protected against experience-based modulations. There are numerous examples in the literature demonstrating innate neuronal machinery that is modulated by experience (e.g., experience-based modulations of ocular dominance columns in V1: Wiesel & Hubel 1965; activation of primary visual cortex during Braille reading in early blind participants: Bucciel et al. 1998; enlargement of the cortical representation of neighboring digits after deafferentation of single digits: Merzenich et al. 1983). Such plasticity, while constrained by the innate connectivity pattern of cortical and subcortical areas, enables the brain to flexibly adjust to a dynamic environment and to both permanent and temporary changes of the input. It is far from obvious why one should assume that a function that is innate would be protected from such plasticity. Thus, although Cook et al. convincingly demonstrate that the properties of MNs can be modulated by experience, the studies discussed in their article are inconclusive regarding the question whether the capability to match visual and motor representations of actions is innate.

We have argued, in another context, that the observed object category-specific organization in the visual ventral stream is driven primarily by distinct long-range connections to downstream processes (Mahon & Caramazza 2011). Different domains of objects are associated with different types of processes. For example, animate but not inanimate objects involve computing affective/social responses. The different processes that characterize different object domains involve distinct, even distant, areas of the brain that must be connected to function effectively as domain-specific networks. On this view, then, visual cortical organization is determined in part by the need to satisfy innate connectivity constraints. The innateness of these constraints is revealed by the fact that the large-scale, domain-specific organization of visual cortex remains invariant in congenitally blind subjects, that is, in the absence of visual input (e.g., Mahon et al. 2009). However, in these subjects the properties of the neurons in “visual” areas have undergone extensive modification: they now respond to completely different sensory inputs even as they retain their domain-specificity. This shows that plasticity does not imply absence of innate neural organization. Likewise, it seems reasonable to assume that the capacity of MNs to match visual and motor representations is made possible by the innate connectivity between ventral premotor cortex/monkey F5 and parietal cortex (AIP [anterior intraparietal], PFG [parietal] areas), which receives visual input from areas IT (inferotemporal cortex), STS (superior temporal sulcus), and MTG (middle temporal gyrus) (Borra et al. 2008; Luppino et al. 1999; Matelli et al. 1986; Muakkassa & Strick 1979; Petrides & Pandya 1984; Webster et al. 1994). This innate connectivity defines the types of processes MNs can participate in while allowing for extensive local plasticity.

In our view, the fundamental question that needs asking is not whether specific associations between visual and motor representations of actions are present at birth – which we take as a given – but whether the link between visual and motor representations takes the form proposed by mirror neuron theorists. A mechanism specialized for connecting visual and motor functions is fundamental for any cognitive function, or otherwise we would lack the ability to react appropriately to sensory input. It seems reasonable to assume that such a basic mechanism should be genetically determined. What remain to be worked out are the anatomical and functional structure of the innate connections between visual to motor representations and the precise nature of the representations involved in this process. In the context of the latter issue, figuring out the role played by MNs in action understanding is key, but as Cook et al. note, the role of these neurons remains poorly understood.