

COMMENTARIES

How does the mirror neuron system change during development?

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This is a commentary on Lepage and Théoret (2007).

It has been suggested that the mirror neuron system (MNS) enables the understanding of others' intentions by simply observing their actions. As Lepage and Théoret's paper highlights, while the MNS has been extensively studied in adult humans and in monkeys, very little is known about its development. What properties of the MNS change during development, or even when in development a functioning MNS is present, is unknown. Lepage and Théoret review the literature and, on this basis, suggest that the MNS is present by infancy. Here, we argue that, even if this is the case, this does not preclude further developmental change. An understanding of how the MNS develops would shed light on its mechanisms and functions.

The notion that actions are intrinsically linked to perception was proposed by William James, who suggested that 'every mental representation of a movement awakens to some degree the actual movement which is its object' (James, 1890, p. 293). The implication is that observing, imagining, preparing, or in any way representing an action excites the motor program used to execute that same action (Jeannerod, 1994; Prinz, 1997). Interest in this idea has grown recently, in part due to the neurophysiological discovery of mirror neurons and, in turn, the mirror neuron system (MNS). Mirror neurons in monkey premotor area F5 and inferior parietal lobule (PF) discharge not only during action execution but also during action observation, which has led many to suggest that these neurons are the neural substrate for action understanding. As Lepage and Théoret's paper highlights, although the MNS has been extensively studied in both adult humans and monkeys, very little is known about the development of the MNS. What properties of the MNS

change during development, or even when in development a functioning MNS is present, is unknown. Lepage and Théoret's paper addresses this latter issue and they suggest that there are sufficient data to conclude that the MNS is present in infancy. However, this does not preclude further developmental change to the MNS, and an understanding of this would shed light on the mechanisms and functions of the MNS.

A recent theoretical account of the MNS predicts that it is the strength of the connections between areas active during action observation that are modulated during development. This theoretical account proposes that the role of the MNS in reading or recognizing the goals of observed actions is best understood within a predictive coding framework (Kilner, Friston & Frith, 2007). The predictive coding framework is a form of recognition model that enables perceptual inference when the mapping between causes and inputs is ill-posed. For example, if while walking along the street someone suddenly waves their arm, are they hailing a taxi or swatting a wasp? In other words, this form of recognition model can infer the goal of an observed action even when the same observed kinematics can be caused by more than one goal or intention. In this type of model, recognition is the inverse of generating sensory data from their causes. Generative models can be framed in terms of a deterministic non-linear generative function:

$$u = G(v, \theta)$$

In the case of action execution/observation, u is the input (the visual signal corresponding to the sight of the executed action) and v is a vector of underlying causes

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(the long-term intentions or goals of the action). $G(v, \theta)$ is a function that generates inputs from the causes given some parameters of the model, θ . The inverse of the generative model is recognition, where the goal is to infer the cause, v , given the data, u . This is called perceptual inference. Importantly, in perceptual inference the model parameters, θ , are fixed quantities that have to be learned. The estimation of these parameters of the generative model corresponds to perceptual learning (see Friston, 2002, 2003, for a detailed account of perceptual learning and inference). In neural models, these parameters, θ , are the between-area connection strengths (Friston, 2002, 2003). In other words, the ability of the MNS to infer the cause of any observed action correctly is dependent upon the between-area connection strengths, which have to be learned. There are two ways in which these connection strengths can be modulated: either new connections can be made *de novo* or the strength of existing connections can be modulated. In the following section we will suggest that during childhood the connection strengths are modulated by the generation of new connections whereas later in development (adolescence) the connectivity is modulated by changes in the connection strengths of pre-existing connections.

In their article, Lepage and Théoret focus on the existence of an MNS in infants. However, there are at least two reasons to suppose that properties of the MNS might continue to develop well beyond infancy. First, some of the brain areas that constitute the human MNS, in particular the inferior parietal cortex, continue to develop well beyond early childhood. Recent MRI studies have shown that the parietal cortex develops throughout adolescence and beyond (e.g. Giedd, Blumenthal, Jeffries, Castellanos, Liu, Zijdenbos, Paus, Evans & Rapoport, 1999; see Blakemore & Choudhury, 2006, for review). Grey matter in the parietal cortex follows an inverted U-shaped pattern of development, with grey matter volume increasing during childhood, peaking at age 10.2 (on average) for girls and 11.8 for boys, and then decreasing during adolescence. This pattern of grey matter development has been attributed to the processes of synaptogenesis during childhood followed by synaptic pruning during adolescence (cf. Huttenlocher, 1979). According to the theoretical account outlined earlier, the period of synaptogenesis during childhood would correspond to making connections *de novo*, whereas the synaptic pruning that occurs during adolescence would correspond to a modulation of the strength of existing connections. Such development might impact on the functions of the developing brain areas – including, for the parietal cortex, MNS functions.

The second reason to speculate that properties of the MNS might continue to develop after childhood has a behavioural basis. Adolescence is a time when peer

relations are of critical importance. It is perhaps more important for adolescents than for adults (or children) to mirror their peers' behaviour; anecdotally, adolescents tend to copy the likes and dislikes of their peers. In this case, it is possible that MNS activity peaks during adolescence. Alternatively, the MNS might not be fully mature by adolescence, and different strategies might be used by adolescents and adults to make sense of others' actions.

Even if the basic capabilities of the MNS do not change during adolescence, it is possible that its interaction with other brain areas (or its responsivity to modulatory influences) might develop. Several neuroimaging studies of the MNS have included a group of typically developing children or adolescents (e.g. Ohnishi, Moriguchi, Matsuda, Mori, Hirakata, Imabayashi, Hirao, Nemoto, Kaga, Inagaki, Yamada & Uno, 2004; Dapretto, Davies, Pfeifer, Scott, Sigman, Bookheimer & Iacoboni, 2006; Lepage & Théoret, 2006; Williams, Waiter, Gilchrist, Perrett, Murray & Whiten, 2006). However, none has directly compared MNS function in children, adolescents and adults. The notion that the MNS might change during childhood and adolescence is currently speculative, and future research is needed to test these predictions.

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Is there evidence of a mirror system from birth?

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This is a commentary on Lepage and Théoret (2007).

Recent neurophysiological, neuropsychological, and behavioral evidence suggests that one of the mechanisms responsible for understanding others' actions is a shared representation mediated by a human homologue of the monkey's mirror neuron system (e.g. Bertenthal, Longo & Kosobud, 2006; Decety & Sommerville, 2004; Frith & Frith, 2006; Grèzes, Frith & Passingham, 2004). The neural circuit responsible for this shared representation could be present from birth or could develop as a function of learning and experience. In the target article by Lepage and Théoret, the authors speculate that a dedicated neural system is present from birth based primarily on evidence of neonatal imitation, although they acknowledge that neurophysiological evidence is required to definitively establish the presence of a mirror neuron system.

We concur with this conclusion, but believe that the evidence for neonatal imitation and how it relates to the development of covert imitation needs to be examined in more detail. In the remainder of this commentary we will discuss how changes in neonatal imitation over real and developmental time support the hypothesis of a functional mirror system from birth. We will also discuss

additional behavioral evidence supporting the presence of this system in somewhat older infants, which suggests that the transition from overt to covert imitation following action observation emerges relatively early in development.

By definition, the mirror system involves the observation of an action directly mapping onto the motor representation of that action. If a specific motor representation is not yet present or is poorly developed, then the observed action will be less likely to stimulate the execution of a comparable response (Calvo-Merino, Glaser, Grèzes, Passingham & Haggard, 2005; Longo, Kosobud & Bertenthal, 2007). This necessity for an internal description or representation of a motor response helps to explain why the imitation of orofacial gestures are such good candidates for imitation via a mirror system. It is well established that fetuses perform mouth opening and closing and tongue protrusion while in utero (Prechtl, 1986). Thus, these gestures are already part of the neonate's behavioral repertoire at birth, suggesting that through practice and exercise a neural network for executing these behaviors has been established. Moreover, the neuro-anatomical evidence shows that the corticobulbar tract

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