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Is there evidence of a mirror system from birth?

Bennett I. Bertenthal[1,2] and Matthew R. Longo[2,3]

1. *College of Arts and Sciences, Indiana University, USA*
2. *Department of Psychology, University of Chicago, USA*
3. *Institute of Cognitive Neuroscience and Department of Psychology, University College London, UK*

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 neuroanatomical evidence shows that the corticobulbar tract

Address for correspondence: Bennett I. Bertenthal, Indiana University, College of Arts and Sciences, Kirkwood Hall, 104, Bloomington, IN 47405, USA; e-mail: bertenthal@uchicago.edu

is already myelinated and innervating the mouth and tongue (Sarnat, 2003). By contrast, the limbs and trunk are innervated by the corticospinal tract which is still unmyelinated at birth. This more advanced level of neural processing available to the tongue and mouth would facilitate the automatic elicitation of the observed response.

Although some reviewers claim that these behaviors are merely reflexive and thus would not necessitate an internal representation, Lepage and Théoret offer some new reasons for concluding that these imitative behaviors are automatic rather than reflexive. In particular, they review evidence showing that the elicitation of orofacial gestures follows both visual and auditory stimuli. These findings are consistent with recent results showing that mirror neurons in nonhuman primates are activated following the perception of either visual or auditory stimuli associated with the action. By contrast, a reflexive response would not be elicited by more than one modality. In addition, it should be noted that the empirical evidence on neonatal imitation suggests that young infants are more likely to match the modeled gesture after it has been presented for some period of time (~40 s), rather than immediately (Anisfeld, 1991). This finding is more consistent with a mirror system in which activation would be expected to build up gradually over time as the gesture is modeled, as opposed to an explanation claiming that the behavior is merely a reflex.

Taken together, this evidence suggests that neonatal imitation is not reflexive; nevertheless, its developmental trajectory is similar to that of many neonatal reflexes, increasing until around 2 months of age, and then declining and virtually disappearing by 5 months of age (Fontaine, 1984; Maratos, 1982).[1] It is during this same window of time that neonatal reflexes are gradually inhibited (McGraw, 1943), suggesting that similar cortical inhibitory processes may serve to suppress spontaneous imitation.

As the automatic elicitation of orofacial gestures becomes suppressed with age, imitation does not disappear entirely. Instead, it becomes subject to volitional control and the infant determines whether or not the observation of these gestures will be followed by their imitation. Recent evidence by Nakagawa, Sukigara and Benga (2003) provides preliminary support for this interpretation. The converse of this result is observed in adults who after experiencing lesions in areas of the frontal lobe involved in inhibitory control begin to display compulsive imitation (Lhermitte, Pillon & Serdaru, 1986). Although overt imitation of facial gestures ceases with the development of inhibition, the presence of a mirror system predicts that covert imitation or simulation would continue and provide specific knowledge about these gestures when observed in others, a claim supported by recent behavioral results in adults (e.g. Bertenthal *et al.*, 2006; Heyes, Bird, Johnson & Haggard, 2005).

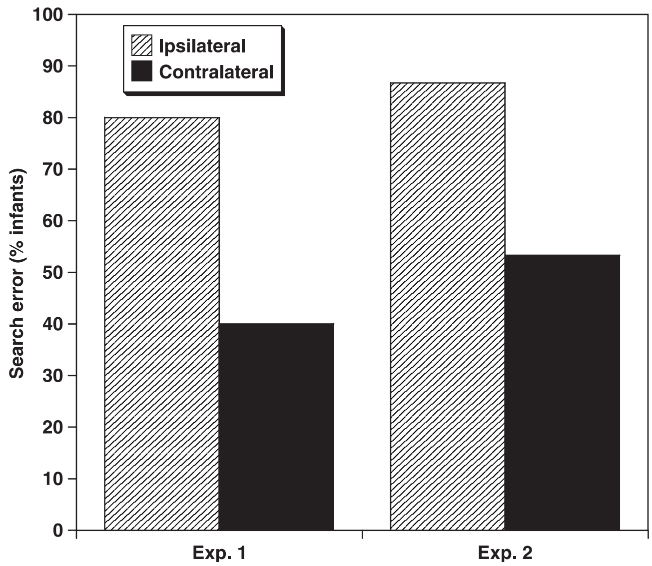

Figure 1 *Percentage of infants searching incorrectly following observation of ipsi- and contralateral reaches by the experimenter in Experiments 1 and 2 (from Longo & Bertenthal, 2006).*

We recently reported evidence for covert imitation in a study testing the A-not-B error in 9-month-old infants (Longo & Bertenthal, 2006). According to a number of researchers (Marcovitch & Zelazo, 1999; Smith, Thelen, Titzer & McLin, 1999), this error is attributable to the formation of a prepotent response created by repetitive searching at one location. If an observation–execution matching system is functional in young infants, then simply observing someone else reach to the same location for a hidden object may be sufficient to elicit this error. By this age we did not expect the observation of an action to elicit overt imitation, but we did expect it to elicit covert imitation, which would be reflected in the perseverative search errors shown by the infants.

The results from two experiments converged to show that 9-month-old infants did show this perseverative error after simply observing an experimenter hiding and finding the object at one location (see Figure 1). Intriguingly, the likelihood of infants showing a perseverative error was significantly greater if the experimenter

[1] In the target article, Lepage and Théoret interpret the empirical evidence as suggesting that neonatal imitation begins to decline by 2 months of age. It is not clear how they reach this conclusion, especially because the developmental evidence presented by Fontaine (1984) clearly shows that imitation of orofacial gestures peaks at 2 months of age. Our interpretation suggesting that imitation peaks at 2 months and disappears at 5 months is based largely on the developmental results presented by Fontaine.

reached for the object with her ipsilateral arm and hand. Most infants tended to reach for the hidden object with their ipsilateral hand, supporting previous observations of an ipsilateral bias in reaching during early development (Bruner, 1969). This finding thus suggests that infants, like adults, are more likely to covertly imitate observed actions if the action is already present in their motor repertoire (cf. Calvo-Merino *et al.*, 2005).

One point which was not emphasized sufficiently by Lepage and Théoret is that the mirror system is important first and foremost for helping to explain the precocious development of action understanding by infants (Bertenthal & Longo, in press). The simulation of perceived actions enables observers to understand not only how the action is organized but the effects of the action as well (Kandel, Orliaguet & Viviani, 2000; Knoblich & Flach, 2001). Recent evidence suggests that this conclusion applies to human infants as well as to adult human and non-human primates. For example, 6-month-old, but not 3-month-old, infants understand that the goal structure of an action is based primarily on the object toward which it is directed (Woodward, Sommerville & Guajardo, 2001). By contrast, the way in which the action is accomplished is less important. If, however, these younger infants are given a few minutes to practice reaching with 'sticky mittens' (allowing them to artificially grasp small objects), then they too show sensitivity to the goal structure of an action (Sommerville, Woodward & Needham, 2005). It thus appears that even minimal experience with a goal-directed action is sufficient for infants as young as 3 months of age to acquire some preliminary understanding of the effects of an action from its motor representation. Currently, it is unclear whether this preliminary motor representation is transient or persists for some extended period of time and could be reinstated with additional motor experiences.

In conclusion, evidence for the very early functioning of the human mirror system is beginning to accumulate, although most of it remains indirect. One of the major challenges for supporting this conclusion is to show some continuity between overt and covert forms of imitation. Until such evidence is provided, the relation between neonatal imitation and later behaviors mediated via an observation–execution matching system will remain quite speculative.

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