Flexibility and development of mirroring mechanisms

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Abstract: The empirical support for the SCM is mixed. We review recent results from our own lab and others supporting a central claim of SCM that mirroring occurs at multiple levels of representation. By contrast, the model is silent as to why human infants are capable of showing imitative behaviours mediated by a mirror system. This limitation is a problem with formal models that address neither the neural correlates nor the behavioural evidence directly.

Hurley's SCM is an ambitious attempt to systematize a large body of recent research. One key prediction is that mirroring should occur at multiple grains, or levels of representation in the motor hierarchy. Recent results from our own lab as well as others confirm this prediction. Several studies have shown that mirroring is dependent on the presence of the observed action in one's own motor repertoire (e.g., Calvo-Merino et al., 2005). We recently used this finding to examine the level of abstraction at which mirroring occurs, and whether this can be manipulated by instructions (Longo, Kosobud, & Bertenthal, in press). We used a paradigm developed previously (Bertenthal, Longo, & Kosobud, 2006) in which participants observe a video image of a hand at rest with fingers spread apart. The hand is shown from the perspective of someone else facing the participant who responds by pressing a button with the right index finger if the stimulus finger appearing farther to the left moves, and with the right middle finger if the finger father to the right moves. With a left hand as the image, the stimulus and response finger match anatomically (e.g., index finger response to an index finger movement); with a right hand, the stimulus and response fingers differ anatomically (e.g., index finger response to a middle finger movement). Responses are faster when there is an anatomical match between the stimulus and response fingers than when there is not, reflecting mirroring, or automatic imitation, of the perceived finger movements.

We used this paradigm to investigate the representational level of abstraction at which mirroring occurs by presenting images of a computer-generated model of a hand, the joints of which could be configured flexibly, allowing us to present finger actions which were either biomechanically possible or impossible. Importantly, the impossible actions were impossible only in terms of the *manner* in which they were performed (i.e., the joints bent in impossible ways), but were perfectly possible in terms of *what* was performed (i.e., tapping a surface). Thus, these actions are impossible at one level of the motor hierarchy (i.e., movements), but possible at a higher level (i.e., goals).

In a first experiment in which no mention was made of different types of movements, comparable automatic imitation of possible and impossible actions was observed, though participants generally were aware of the difference between the stimuli. This suggests that mirroring involves a common representation at the level of goals. In a second experiment, in contrast, in which attention was explicitly drawn to the manner in which the actions were performed by mentioning the two types of movements during instructions, automatic imitation was completely eliminated for the impossible, but not possible, movements. This latter result suggests that actions were being coded at the level of movements. Together, these results demonstrate that mirroring can occur at more than one level of the motor hierarchy, either in terms of goals or in terms of movements, what Rizzolatti et al. (2002) referred to a high- and low-level resonance, respectively.

Similar relations between mirroring and motor ability as described above have also been observed in young infants (e.g., Longo & Bertenthal, 2006; Sommerville, Woodward, &

Needham, 2005). These developmental findings are also relevant to our evaluation of the SCM model because Hurley acknowledges evidence of mirroring by human infants, but her model remains agnostic as to its origins and prerequisites. By contrast, we contend that the evidence reveals that mirroring or imitation is present from birth, but limited to actions already available to infants.

We (Longo & Bertenthal, 2006), for example, used the Piagetian A-not-B error to examine mirroring in 9-month-old infants. This error reflects the tendency of infants at this age to perseverate in searching to a location where they have previously found a hidden object (A), even after having seen it hidden at a new location (B). We found that infants "perseverated" in reaching to the A location, even when they had merely observed an experimenter retrieve the object there, but had not reached themselves. Furthermore, infants were significantly more likely to perseverate when the experimenter had reached ipsilaterally (without crossing the body midline), than when they had reached contralaterally (across the midline). This pattern reflects the difficulty infants of this age show in performing contralateral reaches, what Bruner (1969) referred to as the "mysterious midline barrier", and demonstrates that mirroring in infants – as in adults – is systematically related to motor skill level. While our results show an effect of action observation on motor performance, the flip side of mirroring is reported by Sommerville and colleagues (2005) who show that manipulating infants' ability to perform actions alters their perception of those actions when performed by another agent.

While such results show that mirroring mechanisms are operative quite early in human ontogeny, strong inferences regarding the origins of such abilities must come from studies of younger infants still. In this light, the numerous experiments demonstrating imitation of facial and manual gestures by human neonates are key, suggesting that the neural circuits necessary for mirroring are present at birth. Indeed, given the reported lack of imitation in adult chimpanzees and monkeys, the finding of neonatal imitation in neonates of both species (e.g., Myowa-Yamakoshi, Tomonaga, Tanaka, & Matsuzawa, 2004; and Ferrari et al., 2005, respectively) is especially striking. Such neonatal imitation disappears over the first few months of life in all three species, suggesting that rather than reflecting a precocial social-communicative ability, overt mimicry represents an inability to inhibit automatic priming of motor representations. This pattern highlights the fact that at least some forms of imitation are not abilities reflecting long-term learning over time, but are rather automatic tendencies which must be inhibited in order to interact effectively with the environment.

Thus, there is a clear developmental progression of inhibitory control over mirroring responses. While neonates show overt automatic imitation, reflecting very weak inhibitory control, older infants do not compulsively imitate, but are biased in their overt search behavior by previously observed action. Mirroring in adults is more implicit still, generally manifesting itself in priming of motor responses, rather than their overt imitation (though overt imitation has been reported when attention is diverted [e.g., Chartrand & Bargh, 1999; Stengel, 1947]). This pattern suggests that much of the development of mirroring *responses* reflects changes in inhibitory control, rather than changes in mirroring *representations*, per se.

In conclusion, the model proposed by Hurley is in the tradition of competence vs. performance models. The difficulty with such a model is that it provides a mere skeletal structure that has to be fleshed out be details. Until some critical mass of details has been provided, the validity and usefulness of this model will remain an issue.

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