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Mini review

# Sensorimotor learning and the ontogeny of the mirror neuron system

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## HIGHLIGHTS

- Mirror neurons respond to observation and performance of the same action.
- Response characteristics described with reference to ontogeny and phylogeny.
- Limited evidence for mirror neurons in early development.
- Mirror neuron responses can be modified through experience.
- Sensorimotor experience key to altering and maybe creating mirror neuron responses.

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ABSTRACT

Mirror neurons, which have now been found in the human and songbird as well as the macaque, respond to both the observation and the performance of the same action. It has been suggested that their matching response properties have evolved as an adaptation for action understanding; alternatively, these properties may arise through sensorimotor experience. Here I review mirror neuron response characteristics from the perspective of ontogeny; I discuss the limited evidence for mirror neurons in early development; and I describe the growing body of evidence suggesting that mirror neuron responses can be modified through experience, and that sensorimotor experience is the critical type of experience for producing mirror neuron responses.



## 1. Introduction

Mirror neurons fire when an action is performed and also when the same action, or a related one, is observed [26]. These intriguing neurons have been recorded in ventral premotor area F5 [52] and inferior parietal lobule (IPL) area PFG [25] in the macaque. Mirror neurons responsive to both the production and perception of song have also been found in the forebrain of the swamp sparrow [54]. Direct recordings in humans are limited, but a recent study found mirror neurons in a wide range of brain areas including supplementary motor area (SMA) and parts of the medial temporal lobe [49].

The response characteristics of mirror neurons appear to show that the observed action of another individual activates the same motor programme that the observer would need to use to perform that action. This has given rise to suggestions that mirror neurons acquired their characteristics during phylogeny: that mirror neurons with matching sensory-motor properties are an adaptation for action understanding [3,26]. Alternatively, mirror neurons may develop their characteristics during ontogeny, as a result of experience [33,34]; see also [39,63,64].

An ontogenetic account of mirror neuron properties, such as Heyes' associative sequence learning (ASL) theory [33,34], hypothesises that mirror neurons initially have motor properties but no specific sensory properties (see Fig. 1). They may respond weakly to a range of sensory stimuli but they do not yet respond to the same action as that for which they code motorically. The ASL theory suggests that sensorimotor experience in which there is a contingent or predictive relationship between observed and performed actions will strengthen associations between the sensory and motor representations of an action, producing a motor neuron which responds strongly to the sensory stimulus with which it has been associated. If the association is between the observation and the performance of the *same* action, this motor neuron is now a mirror neuron. Sources of suitable sensorimotor experience for producing mirror neurons include observing one's own actions, being imitated, mirror self-observation, or synchronous action with others (e.g. during dance).

The sensorimotor learning account states that the matching properties of mirror neurons have not been genetically prepared.

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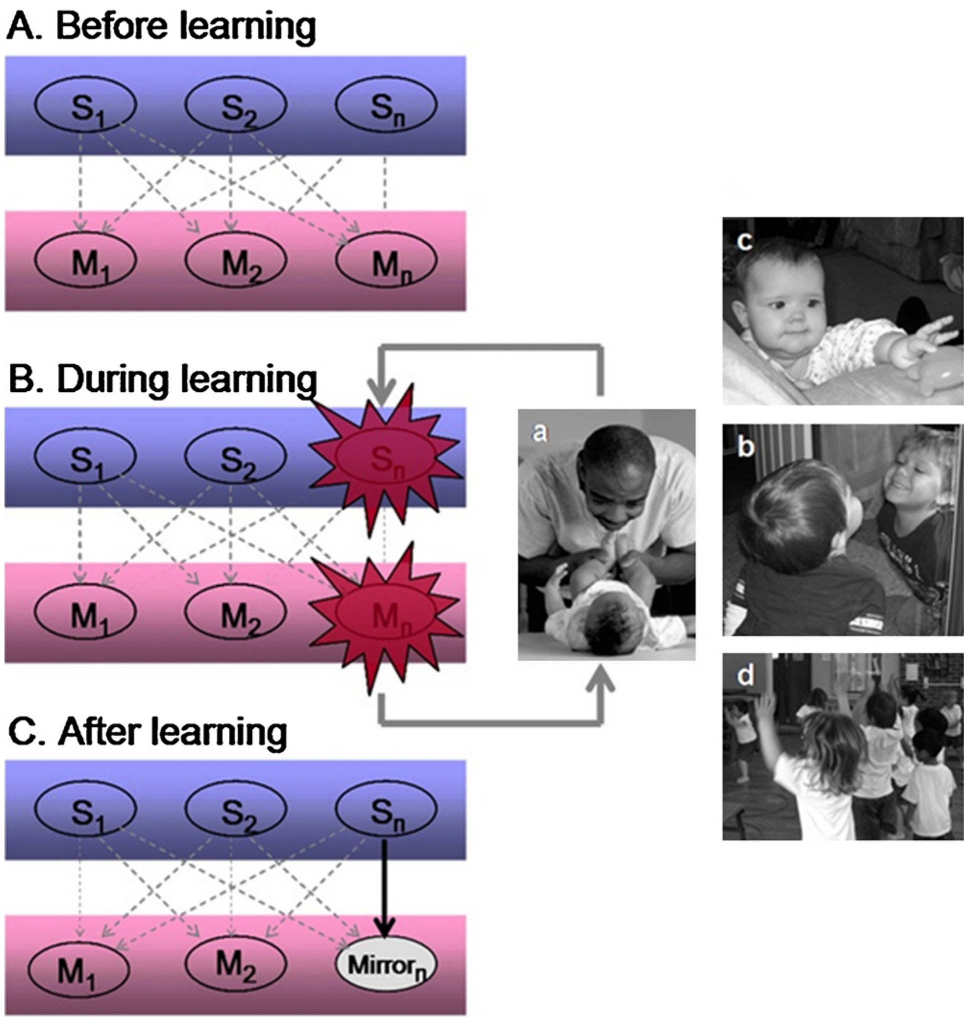


**Fig. 1.** The ASL theory of mirror neuron response properties and imitation. The ASL account suggests that mirror neurons' response properties are acquired as follows: (A) Before learning, sensory neurons with high-level visual properties (e.g. in extrastriate areas) are connected unsystematically to motor neurons with high-level motor properties (e.g. in premotor and parietal cortex). (B) During the type of learning that creates mirror neurons (contingent sensorimotor experience), there is correlated activity of the motor neurons coding for the motor commands required to produce a particular movement and the sensory neurons coding for the sensory properties of that movement. Such experience could be gained through being imitated (a), mirror self-observation (b), observation of one's own movements (c) or synchronous action with others (d). The correlated activity strengthens the connection between the neurons coding for the sensory properties and those coding for the motor commands. (C) After learning, activity in sensory neurons propagates to the motor neurons with which the sensory neurons have strong connections. Thus the motor neurons have become mirror neurons.

Figure reproduced with permission from [34].

This is not to deny that many aspects of sensory and motor systems may be genetically specified. Indeed, genetic preparation for motor control may indirectly provide sources of matching sensorimotor experience via the observation of one's own actions, and thus mirror neurons' properties may build on neural circuits for motor control; but motor control has not evolved in order to produce mirror neurons. To give an analogy, the ability to read English is not genetically prepared. Language appears to be genetically specified, and the ability to read English builds on many neural circuits which have evolved to support language, but language has not evolved in order to support the ability to read.

This paper reviews the data on the ontogeny of the mirror neuron system using a "bottom-up" approach. In Section 2, the response characteristics of mirror neurons are reviewed. This is not intended to be an exhaustive review; rather, I focus on those findings which shed light on possible ontogenetic influences on mirror neuron responses. I then summarise what is known of the early development of the mirror system. Section 4 discusses studies which have used either naturally occurring variations in expertise or deliberate training manipulations to investigate how mirror system responses can be augmented, modified, or even reversed; and the implications of these results for phylogenetic and ontogenetic accounts of mirror neuron properties. I conclude with suggestions for future experiments which could shed further light on this debate.

## 2. Response characteristics of mirror neurons and their relevance to ontogeny

In the first description of mirror neurons, di Pellegrino et al. [52] found that out of the 184 F5 neurons they studied, twelve had "mirror" properties, firing for observation and performance of the same action. A further six neurons had mirror properties and fired additionally in response to actions which were visually similar to those performed, while eleven neurons fired during the observation of actions which were "logically related" to those for which the neuron responded during performance. For example, the most effective visual stimulus for the activation of a logically related neuron could be the placing of food on the table, while motorically, the neuron fired during grasping of the food. The existence of logically