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Sensorimotor learning and the ontogeny of the mirror neuron system

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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.

Keywords: mirror neuron; sensorimotor learning; imitation; associative sequence learning; ontogeny

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

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 program 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 Figure 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).

Figure 1 about here

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

Response characteristics of mirror neurons and their relevance to ontogeny

In the first description of mirror neurons, di Pellegrino and colleagues [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 related mirror neurons can be explained by both phylogenetic and ontogenetic accounts of the acquisition of mirror neuron properties.

Phylogenetically, these properties could have evolved in order to respond to others’ actions with an appropriate action; alternatively, they could have developed ontogenetically in response to repeated experience of seeing food being placed, followed by the monkey grasping the food.

Mirror neurons with a variety of response characteristics have been discovered since 1992. I will devote the body of this section to the discussion of response characteristics which are relevant to the ontogeny of mirror neuron responses. Here, for the sake of completeness, I will briefly mention other interesting response characteristics which have been observed. These include specificity for mouth actions [21], sensitivity to whether actions are performed close to or further away from the monkey [6], response suppression to observed actions [42], sensitivity to mimed grasps [42], view-dependence [5] and sensitivity to the grasped object’s reward value [4].

Another response characteristic which is of interest from an ontogenetic perspective was described by Umiltà and colleagues [61]. 37 of 220 recorded F5 neurons responded during both performance and observation of an object being grasped. On certain trials an object was presented, then hidden behind a screen. Observation of a grasping action towards the hidden object, in which the end point of the action was occluded, caused nineteen of these neurons to fire. These response properties could be explained as an adaptation allowing the monkey to simulate others’ actions even when they are hidden from view; alternatively, they could be due to stimulus generalisation [51]; see also [34] from the situation experienced during ontogeny (object presented, grasp initiated, object-grasp interaction observed) to the testing situation (object presented, grasp initiated). The stimulus generalisation account explains the weaker population response in the hidden object condition

compared to the condition where the object-grasp interaction was visible: less similarity between the learned and tested situations produces a weaker response.

Mirror neurons in the parietal lobe also have properties that have been explained as an adaptation for understanding others (in this case, predicting others' intentions). 165 IPL neurons were recorded during the performance and observation of grasping actions which preceded one of two motor acts: either eating the food or placing it in a container. Around two-thirds of the neurons fired more strongly for the performance of a grasp preceding a certain act (e.g. grasp-to-eat rather than grasp-to-place). Importantly, sixteen of these neurons had matching preferences when observing actions, i.e. they also fired more strongly during the observation of the grasp which preceded the preferred act [25]. The properties of these sixteen neurons could have arisen ontogenetically as a result of repeated exposure to the container as a discriminative stimulus for the trained motor response of placing the food in the container. Thus, when the monkey observed the experimenter grasp the food in the presence of a container, the motor program for grasp-to-place would be activated.

The first data demonstrating a clearly ontogenetic effect on mirror neuron responses came from Kohler and colleagues [41]. These authors described 21 auditory mirror neurons in area F5 which responded both when the monkey heard the sound of paper being torn, and when it performed tearing actions. Since it is unlikely that the sound of paper tearing would have occurred in the environment in which monkeys evolved, it is not possible that there has been selection pressure to respond to this sound with an appropriate tearing action; thus, these response characteristics must have been acquired during ontogeny.

A further demonstration of ontogenetic effects on mirror neuron responses was obtained by Ferrari and colleagues [22]. After four months' experience of observing an experimenter using a tool to manipulate food, 42 out of 209 macaque F5 neurons responded to the observation of tool-use by the experimenter. Interestingly, the majority (31) of these neurons had unspecific motor properties: they fired during the performance of both mouth and hand actions. These neurons could have

acquired their properties via sensory experience of observation of tool use, or via sensorimotor experience in which observation of tool use reliably predicted the performance of a grasp and/or mouth movement. A final example of the role of experience (sensory, motor, or sensorimotor) in the ontogeny of mirror neuron properties was demonstrated by Rochat and colleagues [59]. After macaques had received six months' training to use reverse pliers (in which a grasping action releases an item and a release action grasps the item), eighteen of 282 F5 neurons responded both to the performance and the observation of actions using this tool.

To summarise, the findings from twenty years of mirror neuron research have demonstrated a wide range of response characteristics. Common to all is a relative specificity in terms of the motor response of the neuron; however, the effective sensory input can vary widely. For strictly congruent cells, the only effective sensory input is the observation of the very same action for which the cell codes motorically; but other neurons respond to mimed actions, logically related actions, or the observation of actions performed with tools. Phylogenetic accounts of mirror neuron properties suggest that their basic response characteristics are genetically determined, and that generalisation based on goals can account for responses to tool use, for example. In contrast, ontogenetic accounts suggest that mirror neuron responses are determined by the individual's learning experiences. The ASL theory [33,34] places particular emphasis on contingent sensorimotor experience as a driver of mirror neuron responses. Thus any sensory stimulus which has been experienced in a predictive relationship with a particular motor response has the potential to produce a mirror neuron: that is, a neuron which codes motorically for that particular response but has an effective sensory input determined by the sensory stimulus. The ASL account can explain the wide range of effective sensory inputs to mirror neurons as a consequence of the wide range of stimuli with which their motor responses have been experienced contingently during the individual's learning history.

Early development of the mirror neuron system

Clear evidence in neonates of mirror neurons for a range of actions would constrain ontogenetic accounts of mirror neuron properties. However, no data yet exist describing the presence of mirror neurons in infancy. In lieu of such data, researchers have investigated the imitation of facial gestures in neonatal macaques [24]. Imitation can be used as an indirect index of mirror neuron responses due to the requirement to map the observed action on to the motor program used to perform that action – a mapping which mirror neurons perform; this is supported by findings that repetitive transcranial magnetic stimulation to mirror neuron areas in humans disrupts imitation [11,32,50]. Ferrari and colleagues [24] found that day-old macaques responded to the observation of mouth opening with a lip-smacking movement. While this may demonstrate contingent responses to an arousing stimulus, the lip smacking effect is not specific to the observation of the *same* action, thus cannot be used to conclude that mirror neurons are present at birth. A possible imitation effect was observed in three-day-old macaques: tongue protrusion and lip smacking increased in response to observation of these two actions; however, this effect was very short-lived, being present only on the third day of life, and was not seen at seven and fourteen days of age. Other actions including mouth opening, hand opening, and opening and closing of eyes showed no changes in response to observed actions.

Imitation in human infants has been investigated more extensively. Although a seminal paper suggested that the ability to imitate is innate [47], recent reviews indicate that the only behaviour reliably imitated by neonates is tongue protrusion [1,37,38] and that this effect is not stimulus specific: for example, Jacobson [36] demonstrated an increase in tongue protrusions when a pen or small ball was moved towards the infant. Thus these data can be explained as the result of an oral exploratory behaviour or an innate releasing mechanism for feeding. In summary, in both macaques and humans there are a limited number of behaviours which appear to be imitated at birth, but they are not stimulus-specific and the short-lived nature of the effects means they are unlikely to be mediated by the same neural mechanisms that underlie later imitative abilities. Discussion of the development of imitation in later human infancy is beyond the scope of this paper, but a recent

review [57] suggests that imitation develops in accordance with the amount of sensorimotor experience received by the infant.

Neuroscientific investigation of the developing mirror system is also limited. When investigating mirror responses to observed actions, it is important to know which motor programs are being activated by action observation. Otherwise it is unclear whether the responses are truly “mirror”; that is, whether the motor program which is activated by action observation is the same as, or related to, that which would be used to perform the action. The technique most commonly used in developmental mirror neuron research is electroencephalography (EEG) but this suffers from a lack of specificity (explained below). It has been shown that similar patterns of mu-rhythm desynchronisation occur during action observation as during action execution, in human infants and children ranging in age from 9 months [60] to 8 years [45]; see also [46,48]; and in week-old macaques [23]. While these data, and similar results in adult humans, are thought to indicate that the motor system is modulated by action observation, it is not possible to determine whether *matching* motor programs are activated by the sight of a given action. Without such response specificity, these responses cannot conclusively be attributed to the mirror system (i.e. a system which maps the observed action onto the *same* motor program); rather, they indicate that observed actions are processed, perhaps non-specifically, in the motor system from an early age. This would be a prerequisite for the later development of a mature mirror system through sensorimotor learning (see [34]). In the next section I describe data which support the suggestion that it is this type of learning that gives mature mirror systems their matching properties.

Experience and training effects on human mirror responses

The earliest investigations into the role of experience in the ontogeny of the mirror system capitalised on naturally occurring variations in expertise in the human population. Haslinger and colleagues [31] asked professional pianists and control participants to observe piano playing and non-piano playing finger movements while their blood oxygen level dependent (BOLD) response was

measured using functional magnetic resonance imaging (fMRI). The pianists showed enhanced response to the observation of piano playing movements, in “mirror” areas (i.e. areas thought to be homologous with macaque mirror neuron areas). This effect could be due to the greater sensory experience this group had with the observation of piano playing movements, or the greater sensorimotor experience they had with the observation of these movements during the performance of such movements.

Across two related studies, Calvo-Merino and colleagues [7,8] investigated how differences in visual and motor expertise influence the BOLD response to the observation of complex movements. Participants in the first study were capoeira and ballet dancers. The researchers contrasted the observation of movements with which participants were familiar or unfamiliar (e.g. capoeira dancers observed capoeira moves (familiar) or visually similar ballet moves (unfamiliar)). Responses in mirror areas were greater to familiar than to unfamiliar movements. This contrast, however, confounds visual and motor familiarity: capoeira dancers will have more visual experience, as well as more motor experience, of capoeira moves than of ballet moves. Thus in the second study, female and male ballet dancers observed moves typical of their own or the other gender. Both genders have equal visual experience of both types of move, but motor experience only of their own gender-specific moves. BOLD response was greater to observation of own-gender moves, suggesting that visual experience does not modulate mirror system responses to the same extent as motor experience. However, this experiment does not distinguish between motor and sensorimotor experience as drivers of mirror system responses: over the course of their careers, dancers will have received considerable contingent sensorimotor experience of their own gender’s moves (e.g. through the use of mirrors or observing other troupe members).

Confounds of sensory, motor and sensorimotor experience can be addressed by the use of training experiments in which these different types of experience are systematically varied. The first experiment to investigate the influence of short term training on mirror system responses was

carried out by D'Ausilio and colleagues [18]. Participants, who were all amateur pianists, were asked to learn the left hand part of a piece of piano music over a five day training period. The dependent variable was the size of motor evoked potentials (MEPs) recorded from a left hand muscle during passive listening to the learned piece before and after the training period. MEPs are produced by transcranial magnetic stimulation (TMS) over primary motor cortex; their size reflects the level of activity in the motor cortical representation of the muscle from which the MEP is recorded. Thus the TMS/MEP method allows mirror responses to be measured with far greater specificity than either EEG or (in most cases) fMRI, since the responses of individual muscles to perceived stimuli can be assessed [19,20]. D'Ausilio and colleagues found that, compared with responses before training, MEPs were increased when listening to the learned piano piece, whereas no increase was found for a control piece of flute music. This result suggests that the training created "mirror" associations between the sound of the piano music and the left hand motor commands that would be used to play this piece. However, as the flute piece was not listened to during the training period, this experiment does not rule out the role of purely sensory experience, rather than motor or sensorimotor experience, in producing the increase in MEP size to the listened-to music.

A complementary conclusion can be drawn from the results of Cross and colleagues [16] who scanned dancers repeatedly over a five-week period during which they learned a new modern dance. The researchers found that dancers' reported motor ability to perform the dance was correlated with BOLD response in mirror areas during observation of the dance. Cross and colleagues controlled for purely sensory experience by comparing observation of learned and observed but unlearned dance excerpts, but the driver of the effect they described could still be either motor or sensorimotor experience with the learned dance moves. Another study by Cross and colleagues [17] demonstrated altered ventral premotor responses to abstract cues following sensorimotor experience in which those cues were associated with dance movements; however, this experiment could not rule out motor experience as a driver of this effect.

In order to focus on the role of sensorimotor experience in creating mirror responses, Heyes and colleagues [35] developed what has proven to be a highly fruitful training procedure. Participants were randomly allocated to one of two groups. All participants watched the same videos of two different actions, repeatedly presented on-screen in a random order. The control group received the same type of matching, “mirror” sensorimotor experience they would have gained during a lifetime of watching their own actions and of being imitated: whenever they saw an action they performed that action. The intervention group received non-matching, “counter-mirror” sensorimotor experience: whenever they saw one action (e.g. hand open) they had to perform the other action (e.g. hand close); and vice-versa (e.g. see hand close, perform hand open). The key to this design is that sensory and motor experience was matched across the groups: both saw the same number of videos of each action and both performed each action the same number of times. So any difference between the effects of training in the two groups must be due to the difference in sensorimotor experience between the groups: that is, the contingency or predictive relationship between the observation and performance of the same or different actions. Table 1 illustrates how this training procedure has been used to investigate both imitation and mirror responses across a variety of actions and stimulus types. Here I focus on those experiments which have measured mirror system responses to this type of sensorimotor training.

Table 1 about here

Catmur and colleagues [12] gave participants either mirror or counter-mirror sensorimotor experience of two finger movements. In both groups prior to training, and in the control group after training, MEPs from the index finger muscle were greater during passive observation of index finger movements than of little finger movements; while the little finger muscle showed greater MEPs to little than to index finger movements. This demonstrates that the motor cortex representation of a particular muscle is more active when a movement involving that muscle is observed [20], which is a typical mirror system response [2,40,43]. After counter-mirror sensorimotor experience, however,

this response pattern was reversed: the index finger muscle showed greater MEPs during passive observation of little finger movements than index finger movements, and the little finger muscle showed greater MEPs to index than to little finger movements. This result demonstrates that the response which was associated with the observed action during training is activated during subsequent observation of that action: thus counter-mirror sensorimotor training can reverse mirror system responses to observed actions. This supports the suggestion that mirror responses arise when motor commands and sensory representations are experienced contingently throughout development.

A further experiment by Catmur and colleagues [10] used paired-pulse TMS to test whether the original, pre-training, mirror effect and the post-training counter-mirror effect were supported by the same neuro-anatomical pathways. They found that premotor-M1 connections modulated the response to observed actions for both the mirror and the counter-mirror effects, supporting the claim that counter-mirror sensorimotor training affects the mirror system. Interestingly, connections from both dorsal and ventral premotor cortex to M1 had the same modulatory effect, for both mirror and counter-mirror responses. This finding also suggests that mirror responses, at least in humans, are not restricted to ventral premotor and parietal cortex (homologues of macaque F5 and PFG). Such a result is supported by several fMRI studies of the human mirror system [27,28,62], the findings of mirror neurons in supplementary motor area in humans [49], and mirror-like neurons in macaque dorsal premotor cortex [13]. The most important finding of this study, however, was that the same pathways are involved in both mirror and counter-mirror effects. This confirms the finding of an fMRI study of sensorimotor training which demonstrated a reversal of mirror responses to observed actions in premotor and parietal areas [9].

A potential rapprochement between phylogenetic and ontogenetic accounts of the acquisition of mirror neuron properties was put forward by del Giudice and colleagues [30]. They suggested that evolution has not shaped mirror neuron response properties directly, but instead has canalized the

inputs to the immature mirror system. For instance, they suggest that the tendency for an infant to observe its own actions has evolved not only for motor control but because it provides the immature mirror system with contingent sensorimotor experience of observing and performing actions. This canalization would mean that motor commands for actions are more likely to become associated with the sight of those actions (forming mirror neurons), than with the sight of another action or another type of stimulus. The canalization account predicts that sensory representations of actions will enter into associations with motor commands more easily than will other stimuli. Several experiments have now used the sensorimotor training design to investigate whether there are constraints on the types of stimuli that can enter into associations with motor commands.

Petroni and colleagues [53] gave participants sensorimotor experience in which coloured cues were associated with index and little finger movements. Subsequent observation of the cues alone produced greater MEPs in the muscle of the finger with which each cue had been associated. In a further experiment, the same group demonstrated overlap between BOLD response to observed and performed movements, and cues which had been associated with those movements during sensorimotor training [44]. Most recently, Press and colleagues [55] gave participants sensorimotor training in which they learned to associate different shapes with the performance of certain movements. Observation of a particular shape suppressed the subsequent BOLD response to performance of the movement which had been paired with that shape, but not to performance of other movements (which had been paired with other shapes). This shows that sensorimotor experience can produce sensorimotor responses in motor areas, supporting a sensorimotor account of the development of mirror neurons. However, Press and colleagues also demonstrated that observation of particular shapes suppressed the subsequent response to videos of certain movements in mirror areas. This only occurred for videos of the movements which had been paired with those shapes. This second result indicates that each shape had become associated with the sight of a movement, even though this association was never trained (the videos were not shown during training). The first result suggests that each shape became associated with motor neurons

controlling the trained movement; the second result suggests that these neurons had pre-existing connections to representations of the sight of the trained movement, i.e. that the shapes became associated with *mirror* neurons. Thus it does not appear that there are constraints preventing the formation of associations between non-action stimuli and motor commands. The findings of this study not only provide further support for the theory that mirror neurons arise through sensorimotor learning, but suggest that mirror neurons can flexibly form new associations when the learning environment changes.

Suggestions for future research

The sensorimotor training experiments have been criticised on the grounds that the actions which were trained were non-goal-directed, whereas macaque mirror neurons typically respond to goal-directed actions [58]. Indeed, until recently, a clear difference between the macaque mirror neuron data and human data from TMS and neuroimaging experiments was that the former demonstrate mirror responses to goal-directed actions, while the latter show mirror responses to actions both with and without a goal. However, Ferrari et al. [21] described mouth mirror neurons which responded to actions without a goal, while Kraskov et al. [42] found mirror neurons which responded to mimed actions; thus the conclusion that mirror neurons only respond to goal-directed actions is no longer secure. The sensorimotor account of mirror neuron properties explains this aspect of the difference between monkey and human data by comparing their learning histories: humans receive far more experience of miming actions and performing intransitive movements than do monkeys. Nevertheless, a future line of research should aim to replicate the results of the sensorimotor training experiments using goal-directed actions.

The expertise effects discussed above provided the first evidence that mirror system responses could change as a result of experience. The subsequent training experiments suggest that sensorimotor experience, rather than sensory or motor experience alone, is the critical type of experience for altering – and perhaps for creating – mirror neuron responses. Certain experiments

which could help to clarify this question remain to be carried out. For example, finding mirror neurons for movements for which the monkey had received no sensorimotor experience would support the phylogenetic account of mirror neuron properties. On the other side of the argument, recording human mirror neurons while patients were undergoing sensorimotor training might permit direct confirmation of the suggestion that sensorimotor training can alter or create mirror neuron responses, supporting an ontogenetic account. If mirror neurons do acquire their matching properties through sensorimotor experience it raises new possibilities for the design of training programs to improve imitation and skill learning, and possibly also for improving social functioning, to the extent that this relies on mirror neuron responses.

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Table 1. Experiments using counter-mirror and related sensorimotor training to investigate imitation and mirror system responses.

Authors	Year	Movements and stimuli	Measure	Findings
Heyes, Bird, Johnson & Haggard [35]	2005	Hand opening and closing	Imitation	Counter-mirror training abolishes imitation
Press, Gillmeister & Heyes [56]	2007	Robotic hand opening and closing	Imitation	Mirror training enhances imitation of a robotic hand
Catmur, Walsh & Heyes [12]	2007	Index and little finger abductions	MEPs	Counter-mirror training reverses mirror responses
Gillmeister, Catmur, Liepelt, Brass & Heyes [29]	2008	Hand and foot lifts	Imitation	Counter-mirror training abolishes imitation
Catmur, Gillmeister, Bird, Liepelt, Brass & Heyes [9]	2008	Hand and foot lifts	BOLD fMRI response	Counter-mirror training reverses mirror responses
Cook, Press, Dickinson & Heyes [15]	2010	Hand opening and closing	Imitation	Counter-mirror effects depend on contingency, not contiguity, in accordance with associative learning theory
Petroni, Baguear & Della-Maggiore [53]	2010	Coloured cues; index and little finger abductions	MEPs	Sensorimotor training produces mirror effects to coloured cues
Catmur, Mars, Rushworth & Heyes [10]	2011	Index and little finger abductions	MEPs	Mirror and counter-mirror effects modulated by premotor-M1 connections
Wiggett, Hudson, Tipper & Downing [65]	2011	Hand and foot lifts	Imitation	Counter-mirror effects found with response-outcome sensorimotor experience
Landmann, Landi, Grafton & Della-Maggiore [44]	2011	Coloured cues; index and little finger abductions	BOLD fMRI response	Sensorimotor training produces responses in mirror areas to coloured cues
Cook, Dickinson & Heyes [14]	2012	Hand opening and closing	Imitation	Counter-mirror effects are sensitive to context, in accordance with associative learning theory
Press, Catmur, Cook, Widmann, Heyes & Bird [55]	2012	Coloured shapes; hand movements (point / fist / splay / thumb)	BOLD fMRI repetition suppression	Sensorimotor training produces both motor and mirror suppression to coloured shapes

A. Before learning

B. During learning

C. After learning

Figure 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].