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## Mirroring, association, and the correspondence problem

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### Introduction

Mirror phenomena are behavioral and neurophysiological reactions to social stimuli in which the stimulus and the response match or correspond; they share distinctive features. For example, observation of face-touching and foot-wagging elicit similar, overt behaviors from the observer (Chartrand and Bargh, 1999); observation of arm and hand movements selectively enhance motor-evoked potentials from the muscles involved in performing the same hand and arm movements (Strafella and Paus, 2000); facial expressions of disgust activate the insular cortex, which is also active during presentation of a disgusting smell (Wicker *et al.*, 2003); and the sight of a needle pricking a model's hand activates areas of the anterior cingulate cortex and anterior insula involved in pain processing (Morrison *et al.*, 2004; Avenanti *et al.*, 2005).

In this chapter we consider the extent to which mirror phenomena can be explained in terms of very simple associative processes. We will focus on motoric mirror phenomena, those in which action observation provokes the execution of similar overt or covert motor responses. The first section locates associative accounts of these phenomena among other 'mirror theories', and the second outlines one particular associative hypothesis, the associative sequence learning (ASL) model. The third section reviews evidence that the ASL model is applicable, not only to 'automatic' imitative responses, but also to cases of imitation learning and instructed imitation. In the final section we discuss extension of the ASL model to non-motoric mirror phenomena, and effects that may appear to be beyond its explanatory reach.

### Thoughts about theories

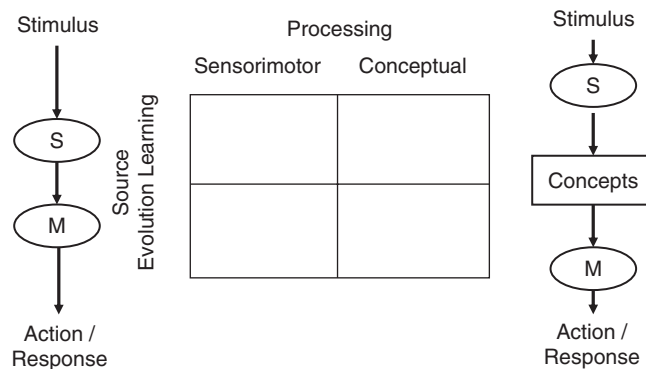
Any hypothesis that purports to explain mirror phenomena (a 'mirror theory') needs to offer an account of their defining characteristic—the match or resemblance between stimulus and response. For example, it needs to explain why observation of hand movement typically elicits hand rather than foot movement, why facial expressions of disgust usually provoke disgust rather than merriment, and why a person who witnesses pain tends to react as if they were in pain rather than, for example, feeling angry. However, a satisfactory account of mirror phenomena must also explain why these relationships are

not invariant; why expansive ‘dominance’ gestures sometimes elicit submissive responses (Tiedens and Fragale, 2003), and why witnessing another’s pain sometimes produces a triumphal, rather than an empathetic, neural response (Singer *et al.*, 2004). Thus, the ‘correspondence problem’ (Brass and Heyes, 2006) has two faces. It challenges us to explain why mirroring happens and, under certain conditions, why it does not.

## Two dimensions

Broadly speaking, mirror theories vary on two dimensions (see Figure 21.1). The first dimension relates to the ultimate source of the information that supports mirroring (Heyes, 2003). Nativist theories suggest that this information was acquired through natural selection and that it is stored in the genome. According to nativist theories, humans are born with a tendency to mirror certain stimuli, or with mechanisms that will support mirror reactions after minimal environmental input. Meltzoff and Moore’s (1997) active intermodal matching hypothesis is a clear and explicit example of a nativist mirror theory. More commonly, nativist assumptions are implicit in statements about the evolutionary history or adaptive function of the mechanisms that mediate mirror phenomena (e.g. Rizzolatti, 2005). In contrast, empiricist theories suggest that the information that is crucial to solution of the correspondence problem comes from interaction between individuals and their environment, especially their social environment, during development. Thus, empiricist mirror theories, such as ideomotor theory, or the theory of event coding (Hommel *et al.*, 2001; Hommel, 2004) emphasize the importance of learning and experience in generating the potential for mirroring.

The second dimension relates to the mechanisms responsible for online mediation of mirror effects. We will refer to the two principal groups of theories that are distinguishable



**Figure 21.1** The dimensions used to classify mirror theories (centre), and schematic representations of the distinction between sensorimotor (left) and conceptual (right) models of mirroring. Sensorimotor models deny that conceptual or ‘higher cognitive’ processing intervenes between activation of sensory (or exteroceptive, S) and motor (or interoceptive, M) representations.

on this dimension as ‘sensorimotor’ and ‘conceptual’ theories. Sensorimotor theories propose that mirroring is mediated by direct excitatory and inhibitory connections between exteroceptive (e.g. visual) sensory representations and motoric or, more broadly, interoceptive representations (see Figure 21.1). The ‘associative sequence learning’ model (Heyes and Ray, 2000; Heyes, 2001) and Keyser and Perrett’s (2004) Hebbian hypothesis (cf. Hebb, 1949) provide clear examples of empiricist sensorimotor theories, and ideomotor theory is arguably another. There is no clearly identifiable example of a nativist sensorimotor theory, but the hypothesis discussed (and dismissed) by Meltzoff and Moore (1989), that imitation is mediated by innate releasing mechanisms, would fall into this category.

In contrast with sensorimotor theories, conceptual theories suggest that, when a mirroring response occurs, some kind of higher-level processing intervenes in a causal chain between stimulus processing and response activation (see Figure 21.1). The nature of this higher-level processing is seldom, if ever, specified. However, it is assumed to vary across categories of mirror phenomenon, and has been given a variety of names. For example, the higher-level processing has been described as ‘semantic’ (Tessari and Rumiati, 2004), ‘symbolic’ (Bandura, 1986), ‘supramodal’, ‘amodal’ (Meltzoff and Moore, 1997), and ‘cognitive’ (Goldenburg, 2006), and as involving ‘appraisal’ (de Vignemont and Singer, 2006). Many conceptual hypotheses are silent about the source of the information that makes higher-order processing possible, and therefore it is not clear whether they are broadly nativist or empiricist.

Building on models of apraxia (Rothi *et al.*, 1991), Rumiati and Tessari’s (2002) two-route model suggests that overtly imitative behavior can be mediated by both sensorimotor and conceptual processing.

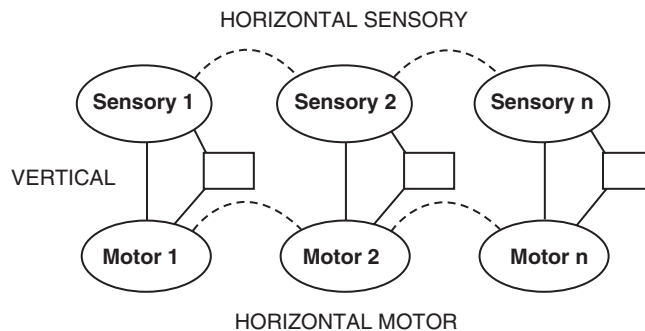
### Associative sequence learning

Two empiricist sensorimotor models make explicit use of associative principles to explain motoric mirror phenomena: the associative sequence learning model (ASL) (Heyes and Ray, 2000; Heyes, 2001) and Keyser and Perrett’s (2004) Hebbian hypothesis. The ASL model predates the Hebbian hypothesis and, although these theories are similar in spirit, they differ in two important respects. First, whereas both theories identify concurrent activation of sensory and motor components as an important condition for associative learning, the Hebbian model is, and the ASL model is not, purely correlative (Heyes, 2005). Within the Hebbian framework, correlated activation of sensory and motor components is sufficient for associative learning. In contrast, and in common with contemporary theories of associative learning in animals (see Pearce and Bouton, 2001, for a review), the ASL model assumes that learning depends on concurrent activation (contiguity) *and* on the extent to which activation of one component predicts activation of the other (contingency). Second, the two theories offer different levels of explanation. The ASL model is couched at a functional level; for example, it refers to sensory and motor representations, but does not make assumptions about their neural implementation. Consequently, although ASL was originally designed to explain overt behavioral

imitation of observed body movement, it can readily be extended to account for other mirror phenomena (see ‘Extending the ASL model to other mirror phenomena’ below). In contrast, the Hebbian hypothesis is a neurobiological model; it seeks to explain motoric mirror phenomena with reference to the formation of connections between the superior temporal sulcus, inferior parietal cortex and area F5 of the monkey premotor cortex (where ‘mirror neurons’ have been located: Rizzolatti *et al.*, 1996). Given its anatomical and physiological specificity, Keysers and Perrett’s Hebbian hypothesis cannot readily be applied to other mirror phenomena.

Ideomotor theory also appeals to associative learning, especially in its incarnation as the theory of event coding (Hommel *et al.*, 2001). The principal claim of this theory is that we are able to imitate the actions of others because our representation of another’s action is similar to our representation of the same action performed by the self. Its weakness, as an account of imitation, is that it does not explain how we are able to imitate perceptually opaque actions, such as facial expressions and whole-body movements, that do not yield similar sensory input when instantiated by self and other. This limitation makes ideomotor theory unsuitable for extension from action mirroring (imitation) to sensation and emotion mirroring because many of these phenomena are opaque, i.e. the mirror stimulus and the mirror response are not perceived by the subject in the same modality or coordinate frame. Thus, although the ASL model, ideomotor theory and the Hebbian hypothesis are mutually compatible, and each has its own strengths and weaknesses, the ASL model is better able to encompass the full range of mirror phenomena.

The gist of the ASL model is very simple (see Figure 21.2). It suggests that motoric mirroring is mediated by excitatory links between sensory (primarily visual) and motor representations of the same behavior, and that these links, or ‘matching vertical associations’, are of two kinds. Direct vertical associations do not involve any intermediate representation, whereas indirect vertical associations link sensory and motor representations via a third representation. For example, a visual representation of a hand gesture (coding how the gesture looks) may be linked to a motor representation of the same gesture (coding what it feels like to perform the action), via another sensory representation (a sound). It is important to note two things about indirect vertical associations. First, by



**Figure 21.2** A schematic representation of the associative sequence learning (ASL) model of imitation.

hypothesis, the third representation either is not conceptual, or does not fulfill its function by virtue of any conceptual properties it may have. Second, indirect vertical associations are thought to function primarily as a means whereby direct vertical associations become established.

Where do vertical associations come from? The ASL model suggests that, whereas a few vertical associations may be innate, the majority are formed through experience that provokes concurrent activation of sensory and motor representations of the same movement. This experience may consist of concurrent observation and execution of the same movement, leading to a 'direct' vertical association, or it may involve exposure to a common stimulus in conjunction with, on some occasions, observation of the movement, and on other occasions with its execution. For example, an infant may hear a particular tapping sound, sometimes when she is hitting a table with her hand, and, at other times, when she sees a caregiver hitting a table in the same way (Jones, 2006). As a consequence of this 'acquired equivalence' experience (Hall, 1996), visual and motor representations of the hitting action will each become linked to a representation of the sound. This 'indirect vertical association' enables activation of the visual representation to be propagated to the motor representation via the sound representation, and, to the extent that it allows the sound concurrently to activate visual and motor representations of the hitting action, to the formation of a direct vertical association between them.

The ASL model addresses the second face of the correspondence problem, explains systematically counter-imitative behavior, with reference to nonmatching vertical associations. Thus, it assumes that links between a sensory representation of one movement and a motor representation of another can be formed in the same way as matching vertical associations, links between sensory and motor representations of the same movement. For example, matching vertical associations are formed when the learner simultaneously sees and executes the same action, whereas nonmatching vertical associations are formed when the sight of one action is regularly paired with the performance of another. The ASL model suggests that, if a system contains more matching than nonmatching vertical associations, and is therefore more prone to imitate than to counter-imitate, this discrepancy is due primarily to the environment in which the system has developed.

The human information-processing system typically develops in an environment that favors the formation of matching vertical associations in a number of ways. First, gross human anatomy is such that many movements of one's own distal appendages can be viewed in much the same way as those of another person. When we watch many of our own hand and finger movements, the appropriate motor representations are activated concurrently with sensory representations, arising from visual feedback, which are similar to the visual percepts that arise when we observe someone else performing the same movements. Second, the typical environment of human development contains optical mirrors and other reflecting surfaces—instruments that allow one's own facial and whole-body movements to be viewed from a third-party perspective—but not video playback devices which provide visual feedback from one movement during execution of another. Third, during early development, humans are surrounded by other humans who imitate them. Leaning over a cot, we coo when the baby is cooing, grimace when the baby

is grimacing (Field *et al.*, 1985; Papousek and Papousek, 1989; Jones, 2006). We do not react to cooing with grimacing, and grimacing with cooing, in a way that would promote the formation of nonmatching vertical associations. Finally, there is language. Generally speaking, the range of movements constituting the referents of each action word look more alike, from a third-party perspective, than those of other action words. Only if natural languages contained words like ‘grint’, referring to you grinning and to me squinting, would the use of language promote formation of nonmatching vertical associations.

As it has been described so far, the ASL model could not explain imitation learning, i.e. imitation of actions that were not in the imitator’s repertoire prior to model observation. To accommodate imitation learning, the ASL model assumes that a novel behavior consists of familiar elements or ‘primitives’ arranged in a novel sequence, and that two kinds of process are initiated when a novel behavior is observed (see Figure 21.2). First, sensory representations of the sequence components are activated and ‘horizontal’ links between them are formed. The model says little about these horizontal links because it assumes that they are not specific to imitation; that they are formed through the same sequence learning processes regardless of whether the novel behavior is imitated, counter-imitated, or merely stored allowing future recognition. However, to the extent that each sensory representation in the sequence is part of a matching vertical association, formation of the horizontal links between sensory representations will allow the second, imitation-specific process to occur. That is, successive activation of each sensory representation, by observation or recollection of the model’s behavior, will provoke activation of matching motor representations in the same order, providing the potential for overt performance of a rough copy of the observed, novel movement. Furthermore, repetitive activation of this sequence of motor representations allows them to become horizontally linked. This horizontal linkage of motor representations constitutes motor learning, produces a new motor primitive, and improves the potential fluidity of imitative movement. Thus, according to the ASL model, imitation learning occurs when matching vertical associations allow sensory input from another’s behavior, rather than feedback from one’s own, to provide the input for motor learning (Heyes, 2003).

## Evidence

### Sources: natural selection versus learning

Evidence of facial gesture imitation in newborn infants (Meltzoff and Moore, 1977) motivated the original claim that imitation is innate, i.e. that natural selection is the source of the information that enables solution of the correspondence problem. This evidence is now undergoing a process of re-evaluation. Having examined all published experimental data on neonatal imitation, Anisfeld (1991, 1996) concluded that it is compelling for only one movement—tongue protrusion. For other candidates, such as mouth opening, lip protrusion, and hand waving, Anisfeld’s analysis suggested that the data were inconclusive, either because too few infants had been tested, or because the reported effects could be artefacts produced by imitation of tongue protrusion. Supporting and extending this view, further experiments have indicated that neonatal

imitation is confined to tongue protrusion (Couturier-Fagan, 1996), have failed to find imitation of tongue protrusion (Ullstadius, 1998), and have suggested that the tongue protrusion effect in early infancy is not sufficiently specific to constitute imitation. The latter studies show that the frequency of tongue protrusion in very young infants increases, not only when they have observed tongue protrusion, but also when they are exposed under comparable conditions to flashing lights (Jones, 1996) or rousing music (Jones, 2006).

In contrast, the results of a number of recent studies suggest that learning is important in relation to imitation. For example, two neuroimaging studies indicate that activation of cortical areas involved in imitation and movement observation depends on learned expertise in performing the observed movements. Using an elegant experimental design, Calvo-Merino *et al.* (2005) presented capoeira dancers, expert classical ballet dancers and nondancer control participants with video clips of closely matched capoeira and ballet movements. The capoeira experts showed stronger activation in the premotor, parietal and posterior STS regions when observing capoeira movements than when observing ballet movements, and the ballet experts showed stronger activation in the same areas when observing ballet movements than when observing capoeira movements. A later study by the same group found greater premotor, parietal and cerebellar activation when male and female ballet dancers viewed moves from their own motor repertoire, compared to opposite-gender moves that they saw frequently but did not perform (Calvo-Merino *et al.*, 2006). This finding suggests that perceptual experience alone is not sufficient to support motor mirroring, and thereby implicates either practice, experience of performing the observed action, or sensorimotor training, experience of concurrently observing and executing the action, as the basis for mirror activation. Because ballet dancers train with optical mirrors, they not only practice same-gender moves more than opposite-gender moves, they also have more sensorimotor experience of the moves specific to their own gender.

Other evidence that learning is important for the development of imitative potential has been provided by studies of musicians. Haslinger *et al.* (2005) found that observation of piano playing was associated with stronger motor activation in pianists than in musically naïve controls, and that the two groups did not differ when observing control stimuli consisting of serial finger–thumb opposition movements. Buccino *et al.* (2004) scanned musically naïve participants while they were observing and reproducing guitar chords. They found activation in the lateral prefrontal cortex just before these novel actions were reproduced, and proposed a model of imitation learning in which the basic motor elements are activated via movement observation and are then selected and recombined, in prefrontal cortex, to match the models action. This hypothesis is highly compatible with the imitation learning mechanism assumed by the ASL model. Here matching vertical associations are automatically activated by movement observation and then combined via horizontal associations. The number and identity of the vertical associations which are activated depends on the motor repertoire of the imitator, while the ability to recombine such elements relies on another set of cognitive mechanisms concerned with serial order processing.

The recent discovery of ‘tool-responding mirror neurons’ in monkey ventral premotor cortex provides further evidence that mirroring depends on learning (Ferrari *et al.*, 2005). Each of these neurons fires when the monkey observes a human using a tool (stick and/or pliers) to secure food, and when the monkey grasps food with its own hand or mouth. Neurons with these properties were found in monkeys that had learned to grasp food and other objects offered to them using a tool, i.e. after numerous training trials in which the animals first observed tool use and then immediately directed a grasping action toward the object held by the tool.

The foregoing studies indicate that learning is an important determinant of mirroring potential, but they do not identify the kind of experience that is crucial. Mirroring potential could depend on repeated observation of actions (perceptual learning), repeated execution of actions (practice) or, as the ASL model predicts, on contiguous experience of action observation and execution, i.e. sensorimotor learning. We investigated this question using a behavioral, ‘automatic imitation’ procedure (Heyes *et al.*, 2005, Experiment 2). In the test phase of this experiment, participants completed a simple reaction time (RT) task in which they were required to open or to close their hand (blocked) as soon as they detected movement of a stimulus hand. In half of the trials the stimulus hand performed a compatible movement (e.g. opened when the required response was hand opening), and in the other half the stimulus hand performed an incompatible movement (e.g. closed when the required response was hand opening). Previous studies had shown that, under these conditions, responding is faster on compatible than on incompatible trials (Stürmer *et al.*, 2000), and that this effect is not due to spatial correspondence between the stimuli and responses (Heyes *et al.*, 2005, Experiment 1). Twenty-four hours prior to the test phase, participants were trained in one of two ways. In a choice RT procedure involving the open and the close hand movement stimuli, the compatible training group was instructed to match the observed actions (e.g. to respond to hand opening by opening their hand) and the incompatible training group was instructed to perform the opposite movement (e.g. to respond to hand opening by closing their hand). Although the training was not extensive (six blocks of 72 trials each), it had a substantial impact on test performance. Like untrained participants, the compatible training group responded faster in compatible than in incompatible trials, but the incompatible training group did not show this automatic imitation effect. Perceptual learning and practice were controlled in this study; the two groups observed and performed the hand movements with equal frequency in the course of training. Therefore, in accordance with the ASL model, the results suggest that automatic imitation depends on sensorimotor learning.

### **Mechanisms: sensorimotor versus conceptual**

#### **Effector effects**

Recent research has begun to identify constraints on imitation—conditions in which healthy adult humans imitate less effectively—and the nature of these constraints is consistent with the view that imitation does not involve conceptual mediation. For example, Vogt *et al.* (2003) reported stronger automatic imitation effects when body movements were viewed from an ‘own person’ perspective (at the angle from which



one views one's own movements) than from an 'other person' perspective (see also Maeda *et al.*, 2002). This is what one would expect if imitation depended on experience of one's own actions *and* on relatively low-level visual representations. If it depended on more conceptual representation, one would expect view independence to be the rule.

Behavioral experiments using the serial reaction time task suggest that conceptual mediation is unnecessary, not only for automatic imitation of familiar actions, but also for imitation learning. In these experiments (Bird and Heyes, 2005; Osman *et al.*, 2005), observers watched a model performing a complex sequence of finger movements in response to an asterisk moving between boxes arranged in a horizontal line on a computer screen. The observers were subsequently required to perform the task themselves under three conditions: when the task was exactly the same as that performed by the model (basic transfer), when the screen stimuli were arranged vertically rather than horizontally (perceptual transfer), and when responses were made with the thumbs rather than the fingers (motor transfer). If the observers encoded what they saw conceptually, if they acquired symbolically coded sequence knowledge by observation, they would be expected to perform well under each of these three conditions. In fact, when compared with controls who had not observed the model, the observers provided evidence of learning in the basic and perceptual transfer tests, but not in the motor transfer test. Similarly, when observational sequence training was followed by tests in which the observers' hands were crossed on the keyboard, there was evidence of imitation learning only when stimulus presentation was programmed such that observers performed the same sequence of finger movements as the model. There was no evidence of imitation learning when the stimulus sequence replicated that presented in the model, and required that response keys be struck in the modeled order, but using a novel sequence of finger movements (Bird and Heyes, 2005, Experiment 2). These findings imply that the observers' imitation learning was effector dependent, that it could not be transferred from fingers to thumbs, or from one anatomically defined sequence of finger movements to another. One would not expect conceptually mediated imitation learning to be effector dependent.

It is important to note that the ASL model, a sensorimotor theory, and conceptual theories do not make symmetrical predictions with respect to the effects of view and effector use on imitation. Conceptual theories predict that imitation will be view and effector independent because they postulate that high-level representations mediate imitation. However, the ASL model does not predict that view and effector dependence will be the norm. Rather, because it assumes that vertical associations can be formed at any level of representation where there is contiguity and contingency between the activation of sensory and motor representations, the ASL model is consistent with both view/effector dependence and independence. Therefore, the findings reported in this section are consistent with the ASL model but not with conceptual theories of imitation.

### Animacy

A number of behavioral studies have reported a marked animacy effect on imitation, i.e. movements of mechanical devices, even when they are robotic (i.e. similar in appearance

to human movements), do not support imitation as effectively as movements of the human body. For example, in a task involving the separation of two parts of an object, Meltzoff (1995) reported that 18-month-old infants completed the task after observing a demonstration by a human adult, but not after a demonstration performed by a mechanical device. In a series of experiments with healthy adults, Castiello *et al.* (2002) found that components of manual grasping movements, such as maximum grip aperture and time to reach peak velocity, were affected by prior observation of a human model grasping an object of the same or different size, and were not influenced by prior observation of a robotic hand/arm performing the same tasks. Similarly, Kilner *et al.* (2003) showed that performance of sinusoidal arm movements in a vertical or horizontal plane was subject to interference from simultaneous observation of another person performing incompatible arm movements, i.e. movement in the orthogonal plane. However, when the model was a full-size robot—with head, trunk, arms and legs—rather than a human, execution of the prespecified movements was unimpaired by simultaneous observation of incompatible responding.

Neurophysiological studies have also found stronger motoric mirror effects when participants observe human actions rather than movements of a mechanical device. Single-cell recording has shown that mirror neurons in area F5 of the monkey premotor cortex fire when the monkey grasps an object and when it observes a human hand grasping the same object, but not when the monkey sees the object grasped by a mechanical pincer (Gallese *et al.*, 1996). Similarly, PET has detected significant activation in the left premotor cortex when human participants observed manual grasping actions performed by a human model, but not when they were performed by a robotic hand/arm (Tai *et al.*, 2004).

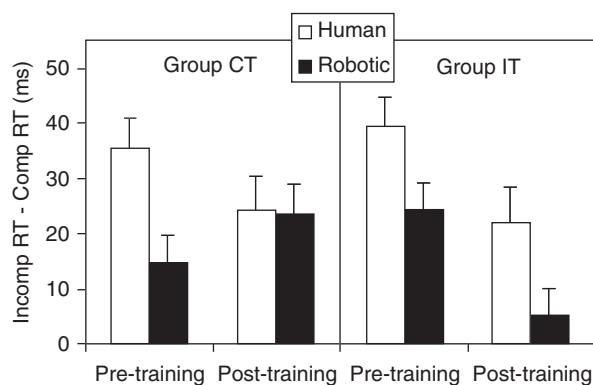
Sensorimotor and conceptual models of imitation offer contrasting explanations for animacy effects. Postulating sensorimotor mechanisms, the ASL model suggests that human movements are more effective than mechanical movements as stimuli for imitation because, in humans, the potential to imitate is based on experience in which we concurrently observe human movement (our own, and that of others) and perform similar movements ourselves. According to this view, if a child was surrounded by sophisticated robots in the course of development, they would imitate robotic movement as effectively as human movement. In contrast, conceptual models would, presumably, explain animacy effects with reference to the different meanings of human and robotic stimuli. For example, a model of this kind might suggest that conceptual processing, after detection of a robotic movement stimulus, results in that stimulus being classified as inanimate, and blocks activation of a corresponding motor representation.

We have conducted a series of experiments testing the ASL model's sensorimotor account of animacy effects. These experiments used the hand opening and closing compatibility paradigm described above (see 'Sources: natural selection versus learning' above; Heyes *et al.*, 2005). The first experiment showed that this example of automatic imitation is susceptible to an animacy effect, and that this effect is not due to low-level perceptual features of the stimuli (Press *et al.*, 2005). Participants were required to perform a prespecified movement (e.g. opening their hand) on presentation of a human or robotic hand in the terminal posture of a compatible movement (opened)

or an incompatible movement (closed). Both the human and the robotic stimuli elicited automatic imitation; the prespecified action was initiated faster when it was cued by the compatible movement stimulus than when it was cued by the incompatible movement stimulus. However, even when the human and robotic stimuli were of comparable size, color and brightness, the human hand had a stronger effect on performance.

The second experiment used a training procedure, simulating the situation in which a child grows up among robots (C. Press, H. Gillmeister and C. M. Heyes, unpublished data). Participants completed the simple RT task described above before and after a period of compatible or incompatible training in which they responded to robotic stimuli in a choice RT task. The compatibly trained group responded to an open robotic stimulus by opening their hand and to a closed robotic stimulus by closing their hand, whereas the incompatibly trained group were instructed to use the reverse stimulus–response mappings. As predicted by the ASL model, compatible training eliminated the animacy effect (see Figure 21.3). Before compatible training with robotic stimuli, the compatibility effect was substantially larger for human than for robotic stimuli, but after compatible training the magnitude of this effect did not vary across stimulus categories. If compatible training eliminated the animacy effect solely by providing perceptual experience of the robotic stimuli, or practice in performing the response movements, one would expect incompatible training to have had a similar effect. In fact, incompatible training did not change the magnitude of the animacy effect, suggesting, in line with the ASL model, that it is contingent experience of observing and executing the same action that establishes the sensorimotor links which mediate imitation.

Empiricist conceptual models would allow that the meaning of robotic stimuli could change through experience; for example, that through interaction with a robot we could come to believe that it has mental states. However, the foregoing study did not give



**Figure 21.3** Mean compatibility effect (RT on compatible trials minus RT on incompatible trials) before and after training, when stimuli were human (white bars) or robotic (black bars) hands. In training, Group CT responded to open robotic hands by opening and to closed robotic hands by closing their own hands, whereas Group IT responded to open by closing, and to closed by opening.

subjects the kind of experience that one would expect to induce conceptual change, and there is no reason to believe that, after compatible training, participants had revised their beliefs about robots. Therefore, by examining the effects of learning on imitative performance, this study provides indirect but compelling evidence that animacy effects can be mediated solely by sensory and motor representations.

### Goals

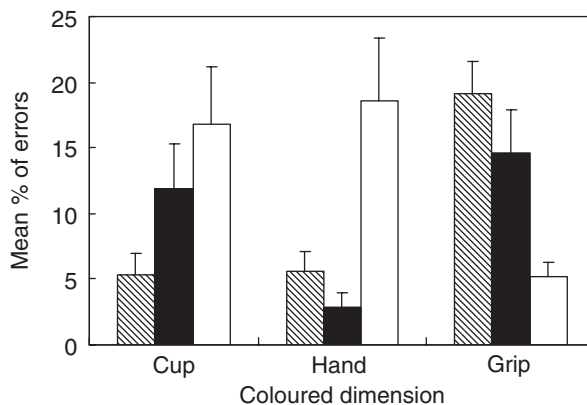
Potentially the strongest evidence in favour of conceptual models of imitation comes from studies suggesting that, when instructed to imitate, children and adults prioritize the reproduction of ‘goals’, the effects of actions on objects, over the reproduction of ‘means’, choice of effector and movement path. Several of these studies have used the pen-and-cups task. On each trial in this speeded response procedure the participant confronts a model as the latter moves a centrally located pen into one of two colored cups (object), using his right or his left hand (effector), while grasping the pen with his thumb pointing up or down (grip). Both when they are required to mirror imitate (e.g. to copy right-hand movements with the spatially compatible left hand) and to transpose (e.g. to copy right-hand movements with the spatially incompatible right hand), participants make fewer cup errors than hand errors, and fewer hand errors than grip errors (Wohlschläger and Bekkering, 2002; Avikainen *et al.*, 2003).

The goal-directed theory of imitation (GOADI; Gattis *et al.*, 2002; Wohlschläger *et al.*, 2003) explains the cup < hand < grip error pattern with reference to conceptual processes that intervene between stimulus processing and response activation. Specifically, GOADI suggests that ‘the perceived act is cognitively decomposed into separate aspects’, selected aspects or ‘goals’ are hierarchically organized, with ends taking priority over means, and then, through the ideomotor principle, selected goals elicit the motor programme with which they are most strongly associated (Wohlschläger *et al.*, 2003). This conceptual hypothesis appeals to the meaning, or functional significance, of stimulus components to explain why some are imitated more accurately than others. In contrast, the ASL hypothesis, a sensorimotor model, attributes biases in imitation to (1) input factors—variables affecting stimulus processing, (2) experience—the individual’s history of learning, and (3) output factors—variables, such as task instructions, that influence whether activation of a motor representation is inhibited or expressed in overt behavior. In the case of the cup < hand < grip error pattern, input factors are the most plausible candidate. In all previous experiments involving the pen-and-cups task, the two cups were of different colors, whereas the hands and grips were, naturally, of the same color. Differential coloring of the cups could have reduced cup-errors by heightened the salience of the cups or by making them more discriminable than the hands or the grips.

To test this hypothesis, Bird, Brindley, Leighton and Heyes (in press, Experiment 2) gave two groups of participants the pen-and-cups task. For one group, the cups were colored red and blue, as in previous experiments. For the other group, the cups were of the same neutral color, but the model’s hands were colored—she wore a blue glove on one hand and a red glove on the other. As predicted by the sensorimotor account, the cup < hand < grip error pattern was replicated in the cups-colored group but not in the

hands-colored group. When the model wore gloves of different colors, participants made fewer errors in hand selection than in cup or grip selection.

Although predicted by the sensorimotor account, this result can also be explained by GOADI, a conceptual model. Shifting the color cue from the cups to the hands may have reduced hand errors (and increased cup errors), not by increasing the probability that participants would detect which cup had been moved in each trial, but by provoking them to revise their 'goal hierarchy'. For example, they may have inferred that the colored dimension was, in the context of the experiment, the most important stimulus dimension to imitate accurately, and this inference may have contributed to conceptual processing between stimulus detection and motor activation. Post-test questionnaire responses were inconsistent with this interpretation, showing that the colored dimension was judged to be the easiest to imitate but not the most important. However, to test the conceptual account more rigorously, J. Leighton, G. Bird and C. M. Heyes (unpublished data) used a 'geometric' version of the pen-and-cups task. Instead of watching a video in which a human model demonstrated each action to be performed, participants responded to a flashing array of geometric shapes on a computer screen. For example, when the trial began with successive flashing of (1) a square on the left of the screen, (2) the 'inside' rectangle attached to that square, and (3) the ellipse on the right of the screen, subjects were required to grip the pen between the index and middle fingers of their right hand, and to place it in the cup on their left. In terms of its low-level stimulus properties, the geometric array was matched with model demonstration, but the geometric stimuli could not be meaningfully parsed into 'means' and 'ends'. Therefore, the sensorimotor account predicted that the error patterns observed in previous pen-and-cups experiments would be replicated in the geometric version, whereas GOADI, which ascribes them to conceptual, goal-related processing, predicted that they would not. As Figure 21.4 indicates, the predictions of the sensorimotor model were correct. In the geometric task, there were minimal cup errors when the cups were colored, minimal hand errors when the hands were colored, and minimal grip errors when the grips were colored.



**Figure 21.4** Mean percentage error (plus standard error of the mean) in the geometric pen-and-cups task, when the cups, hands or grips were of different colors. Cup selection errors are represented by hatched bars, hand selection errors by black bars, and grip selection errors by white bars.

## How far can you go with associative learning?

### Extending the ASL model to other mirror phenomena

The ASL model of action mirroring can be extended to account for a range of mirror phenomena reported in the literature. These phenomena are of three principal types: action mirroring (imitation), sensation mirroring, and emotion mirroring (emotional contagion/empathy). Because it has both sensory and affective components, empathetic pain straddles the boundary between the second and third categories. Using empirical examples of sensation and emotion mirroring, the following paragraphs indicate, in broad outline, how the ASL hypothesis can be extended to other mirror phenomena.

It has been shown that action mirroring can be explained with reference to ‘vertical links’, formed through associative learning, between ‘sensory’ (visual, auditory) representations of action, and the observer’s internal ‘motor’ representations of a matching action. Once established, these vertical links allow activation of the sensory representation of an action (caused by action observation), to be propagated to the motor representation, which increases the probability that the observed action will be performed. In the basic ASL model, ‘motor’ representations were characterized as comprising both somatosensory information and motor commands (Heyes and Ray, 2000). To extend the model, it is necessary to emphasize their interoceptive sensory function. Thus, in an extended version of the model, the representation that mirrors would be characterized as an ‘interoceptive’ representation, coding what it ‘feels like’ to perform an action/to be touched/to be disgusted. The content of the representation initially activated by model observation would remain the same—it would code information about a social partner derived from the distal senses—but it would be described as an exteroceptive representation.

Evidence for sensation mirroring in the human brain has been provided by two recent studies investigating the neural response to observation of touch using fMRI (Keysers *et al.*, 2004; Blakemore *et al.*, 2005). Participants were either touched themselves, or observed another individual being touched. Both studies revealed overlapping activation of the secondary somatosensory cortex when participants were touched and when they observed another being touched. Furthermore, Blakemore *et al.* (2005) found somatotopic activation of the primary somatosensory cortex when participants were touched and observed another being touched. Thus, observation of touch causes the somatosensory cortex to become activated as if the individual had been touched. These effects can be explained by suggesting that an exteroceptive visual or auditory representation of touch is associated with the interoceptive sensory representation of what it feels like to be touched. This kind of association could be formed when the individual observes themselves being touched.

Emotional mirroring has been reported in a number of studies (e.g. Wicker *et al.*, 2003; Morrison *et al.*, 2004; Singer *et al.*, 2004). In the study by Wicker *et al.* (2003), fMRI was used to study brain activity while participants either inhaled disgusting odorants, or viewed the facial expression of another individual who had inhaled the same odorants. As expected, participants who experienced disgust after inhaling the odorant showed activity in the insula (Zald and Pardo, 2000), but, interestingly, overlapping insula activity

was also seen when participants viewed the disgusted facial expressions of another. Thus, observing indications of disgust in another (a disgusted facial expression) activated the same neural areas as when the participants experienced disgust themselves. This example of emotional mirroring can also be explained within the ASL framework if one supposes that vertical links can be formed between exteroceptive visual (a disgusted facial expression), or auditory (the 'yuck' sound in English), representations of disgust, and the interoceptive emotional representations of disgust. Associations between the exteroceptive and interoceptive representations of disgust may be formed when two individuals react to a common disgusting stimulus. In this example, each individual will have co-activation of their interoceptive emotional disgust response and of the exteroceptive visual and auditory disgust representations through observing the response of the other.

### Challenges for the future

It is notoriously difficult to evaluate claims regarding the sources—natural selection versus learning—of information. To support their claims, nativist mirror theories concentrate on studies of very young infants, and empiricist mirror theories focus on the effects of training and expertise. However, neither the appearance of a phenomenon in early development, nor its susceptibility to change through learning, provide definitive evidence regarding the source(s) of the information that solves the correspondence problem. Research with very young infants is especially difficult to conduct and to interpret, and some innate tendencies are subject to change through learning. Therefore, it would be helpful to investigate the putative sources themselves; to know more about the selection pressures that have, according to nativist theories, shaped an innate capacity for mirroring, and about the developmental environments which, according to empiricist theories, support the learning that provides mirroring potential. The second of these challenges, to find out more about the environment of human development, is more tractable than the first, to find out about the environments of our evolutionary ancestors, but the developmental challenge is still formidable. Most research in psychology and neuroscience examines isolated systems, systems that have been pulled out of their natural environments and isolated, if not on a laboratory bench, then in a laboratory cubicle. In contrast, the kind of developmental research needed to sharpen the predictions and explanatory power of empiricist mirror theories requires observation of humans at all stages of development in their natural environments. Not just individuals, but their environments, need to be put 'on the bench'.

More familiar, but equally difficult, challenges must be met in order to test sensorimotor against conceptual accounts of mirroring. Some of these challenges are analytic, requiring the forging and maintenance of subtle distinctions, while others are empirical, requiring the development of ingenious experimental methods. On the analytic side, we need to distinguish conceptual mediation from other putative, higher-level effects on mirroring. 'Conceptual mediation' refers to the hypothesis that mirroring is achieved via a causal chain of processes in which some kind of higher-level processing is applied to the output of exteroceptive sensory processing, and it is the output from this higher-level analysis that causes activation of an interoceptive, or mirror, representation

(see right side of Figure 21.1). There are at least two ways in which higher cognition could influence mirroring without constituting conceptual mediation thus defined. First, higher cognition could modulate activation of an exteroceptive representation. For example, when participants are told that a moving dot represents movement of a human arm, they may be more likely to imagine those movements, and therefore show a stronger automatic imitation effect, than when they are told that the dot movements were computer-generated (Stanley, Gowen and Miall, in press). Second, higher cognition could have an independent influence on activation of an interoceptive representation. In this case, higher cognition would have an impact on activation of the exteroceptive representation via a route distinct from the 'vertical link' connecting the exteroceptive and interoceptive representations. For example, when I see a friend waving at me through a window, my knowledge that I am in an interview situation may lead me to inhibit the interoceptive activation caused by the sight of the waving friend.

Research on mirroring is just getting underway. Many sensation- and emotion-mirroring phenomena were demonstrated for the first time in recent years, and, although imitation has been studied for more than a century, it has made substantial progress only in the last decade. It is likely to be difficult, but also rewarding, to find out exactly how the correspondence problem is solved.

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