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Mirroring 'meaningful' actions: Sensorimotor learning modulates imitation of goal-directed actions

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Abstract

Imitation is important in the development of social and technological skills throughout the lifespan. Experiments investigating the acquisition and modulation of imitation (and of its proposed neural substrate, the mirror neuron system) have produced evidence that the capacity for imitation depends on associative learning in which connections are formed between sensory and motor representations of actions. However, evidence that the development of imitation depends on associative learning has been found only for non-goal-directed actions. One reason for the lack of research on goal-directed actions is that imitation of such actions is commonly confounded with the tendency to respond in a spatially compatible manner. However, since the most prominent account of mirror neuron function, and hence of imitation, suggests that these cells encode goal-directed actions, it is important to establish whether sensorimotor learning can also modulate imitation of goal-directed actions. Experiment 1 demonstrated that imitation of goal-directed grasping can be measured while controlling for spatial compatibility, and Experiment 2 showed that this imitation effect can be modulated by sensorimotor training. Together, these data support the hypothesis that the capacity for behavioural imitation and the properties of the mirror neuron system are constructed in the course of development through associative learning.

Imitation – copying the topography of body movement, the way in which parts of the body move relative to one another – is thought to underlie the early development of a range of communicative and instrumental behaviours as well as supporting social learning throughout the lifespan (Frith & Frith, 2012; Legare & Nielsen, 2015). How humans acquire the capacity to imitate others, however, has been the source of considerable debate. A series of high-profile developmental studies initially suggested that infants may be equipped from birth with the capacity to imitate facial and hand actions (Meltzoff & Moore, 1977; Meltzoff & Moore, 1983, 1989). If correct, this would suggest that the ability to imitate others is a special-purpose cognitive module which is genetically inherited (Meltzoff & Decety, 2003; Oberman, Hubbard, & McCleery, 2014). However, the studies of newborns have been challenged on a number of grounds, including by evidence that neonatal imitation may be limited to one action, tongue protrusion (Anisfeld, 1979; Ray & Heyes, 2011); by the suggestion that such 'imitation' may in fact be an arousal response (Jones, 1996, 2006); and, most recently, by a

large-scale longitudinal study which found no evidence for neonatal imitation and indicated that previous positive results were due to methodological and statistical artefacts (Oostenbroek et al., 2016).

An alternative to the nativist account, the associative sequence learning (ASL) model of imitation, is based on the body of knowledge accumulated primarily through research on conditioning and associative learning in animals (Mackintosh, 1974, 1983, 1994). According to the ASL model, the capacity to copy the topography of observed actions depends on sensorimotor associations that are formed in everyday life when infants are imitated by adults, during exposure to optical mirrors, when children and adults engage in synchronous activities, and via

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acquired equivalence experience of the kind provided by action words (Catmur, Walsh, & Heyes, 2009; Heyes, 2001). Each of these associations comprises bidirectional excitatory links between a sensory (typically visual) representation of an action and a motor representation of the same action.

Over the past decade, considerable evidence has accumulated to support the suggestion that associative sensorimotor learning underlies both the capacity for imitation (Cook, Dickinson, & Heyes, 2012; Cook, Press, Dickinson, & Heyes, 2010; Gillmeister, Catmur, Liepelt, Brass, & Heyes, 2008; Heyes, Bird, Johnson, & Haggard, 2005; Press, Gillmeister, & Heyes, 2007; Wiggett, Hudson, Tipper, & Downing, 2011) and the development of the proposed neural substrate of imitation, the mirror neuron system (Catmur et al., 2008; Catmur, Mars, Rushworth, & Heyes, 2011; Catmur, Walsh, & Heyes, 2007; Cavallo, Heyes, Becchio, Bird, & Catmur, 2014; Landmann, Landi, Grafton, & Della-Maggiore, 2011; Petroni, Baguear, & Della-Maggiore, 2010; Press et al., 2012). Typically, these experiments have exposed adults to novel sensorimotor contingencies – through training in which the performance of an action is paired with observation of an alternative familiar action ('counter-mirror' training), a novel action or a non-action stimulus – and found that this experience has a profound impact on behavioural and neurophysiological indices of imitation. (For similar findings in human infants and non-human animals, see de Klerk, Johnson, Heyes, & Southgate, 2015; Mui, Haselgrove, Pearce, & Heyes, 2008; Range, Huber, & Heyes, 2011.) For example, a relatively short period (1-2 hr) of counter-mirror training (e.g., observation of little finger abduction paired with performance of index finger abduction, and vice versa) can abolish 'automatic' imitation of the trained responses and reverse neural mirroring. Furthermore, functional imaging and recording of motor-evoked potentials indicate that whereas action observation normally induces activity in corresponding areas of motor cortex (e.g., observation of little finger movement activates regions controlling little finger movement), after counter-mirror training action observation induces activity in non-corresponding areas (e.g., observation of little finger movement activates regions controlling *index* finger movement) (Catmur et al., 2008; Catmur et al., 2011). Abolition and reversal effects of this kind are what one would expect if, as the ASL model suggests, imitation is normally based on bidirectional excitatory links between sensory and motor representations of the same action (e.g., between visual and motor representations of little finger abduction), and counter-mirror training establishes both parallel inhibitory associations and excitatory links between nonmatching sensory and motor representations (e.g., between a visual representation of little finger movement and a motor representation of index finger movement).

However, to date, the effects of sensorimotor associative learning on imitation and mirror neuron responses have been demonstrated only for intransitive actions such as finger abduction, hand opening and foot lifting that are not directed towards a distinctive object in the environment. (In conformity with contemporary literatures on imitation and mirror neurons, we refer to actions that are directed to objects as 'goal-directed' and to those that are not directed to objects as 'non-goal-directed'. However, given the ambiguity of the word 'goal' (Cook, Bird, Catmur, Press, & Heyes, 2014), which is used to refer to both intentional and physical objects, the terms 'transitive' and 'intransitive' would be preferable.) This could be problematic for a fully comprehensive account of the development of the ability to imitate because the most prominent account of mirror neuron function, and hence of imitation, suggests that these cells selectively encode goal-directed actions (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti & Fogassi, 2014; Rizzolatti & Sinigaglia, 2010, but see Cook & Bird, 2013; Cook et al., 2014 for opposing views). For example, some of the studies demonstrating that counter-mirror sensorimotor learning can reverse mirror neuron responses to observed actions have been criticised on the grounds that the trained actions (in this case, abduction movements of the index or little finger) were 'meaningless', i.e., non-goal-directed (Rizzolatti & Sinigaglia, 2010, p. 270). Therefore, it is important to establish whether sensorimotor associative learning can also modulate imitation of goal-directed actions.

One reason for the lack of research on how learning can modulate imitation of goal-directed actions is that when actions are directed to objects, it is difficult to distinguish imitation from spatially compatible responding. In other words, when participants observe a model performing a goal-directed action, it is hard to tell whether they are copying the way in which parts of the body move relative to one another or merely responding at the same location as the model. For example, Bekkering and colleagues (Newman-Norlund, Ondobaka, van Schie, van Elswijk, & Bekkering, 2010; Newman-Norlund, van Schie, van Zuijlen, & Bekkering, 2007; van Schie, van Waterschoot, & Bekkering, 2008) investigated goal-directed imitation using a task in which participants performed power (whole-hand) or precision (finger-thumb) grips on a manipulandum comprising a large cylinder (which had to be grasped with a power grip) positioned below a small cylinder (which had to be grasped with a precision grip). Participants were faster to perform a power grip when they observed an actor also performing a power grip on a similar manipulandum than when they observed the actor performing a precision grip, and similarly, they were faster to perform a precision grip when they observed a precision than when they observed a power grip. This pattern of response times is consistent

with imitation – participants may have copied the spatial relations among the fingers and thumb that characterise power and precision grips, respectively – but it could also have been due to up/down spatial compatibility: for example, facilitation of responses in the upper part of the task space when observing an action performed in the upper part, rather than in the lower part, of visual space. Imitation cannot be isolated from spatial compatibility in this and similar tasks because precision grips are always performed and observed in the upper part of space, whereas power grips are always performed and observed in the lower part of space. Thus, 'imitatively compatible' responses (e.g., perform precision grip while observing precision grip) are also spatially compatible (e.g., perform response in the upper part of space while observing action in the upper part of space), and 'imitatively incompatible' responses (e.g., perform precision grip while observing power grip) are also spatially incompatible (e.g., perform response in the upper part of space while observing action in the lower part of space). This is a concern because analogous effects of horizontal (left-right) spatial compatibility have been found to contaminate measurement of imitative compatibility using non-goal-directed actions (e.g., Catmur & Heyes, 2011).

To dissociate imitative and spatial compatibility, this study used a modified version of the task developed by Newman-Norlund et al. (2010). In every trial, participants were instructed to perform a power or precision grip on a manipulandum which, like the Newman-Norlund manipulandum, could be grasped with a power grip in the lower part of task space and a precision grip in the upper part of task space. On every trial, participants observed an actor grasping the same manipulandum with either a power or precision grip. However, crucially, in half of the trials, the observed manipulandum was inverted such that the actor performed a power grip in the upper part of the visual space or a precision grip in the lower part of the visual space. In these trials, imitatively compatible responses (e.g., perform precision grip while observing precision grip) are spatially incompatible (e.g., perform response in the upper part of space while observing action in the lower part of space), and imitatively incompatible responses (e.g., perform precision grip while observing power grip) are spatially compatible (e.g., perform response in the upper part of space while observing action in the upper part of space). Therefore, the design of this study controls for any contribution of up/down spatial compatibility to previously reported imitation effects and allows us to isolate any effect of imitative compatibility from that of spatial compatibility.

Experiment 1 tested whether imitation of goal-directed grasping actions could be measured while controlling for spatial compatibility, and Experiment 2 tested whether this imitation effect could be modulated by counter-mirror associative sensorimotor learning.

Experiment 1

Method

Participants. Sixteen right-handed participants (two males) aged 18-25 years (mean = 21.0 years, standard deviation [*SD*] = 2.0) were recruited via the University of Surrey experiment participation pool. Participants received course credit or a small honorarium for their time. Experimental procedures were approved by the University of Surrey Ethics Committee and followed the Declaration of Helsinki.

Apparatus. Participants sat at a table in a quiet experimental cubicle. At the edge of the table, aligned with and 10 cm from the participant's chest, was a cardboard occluder (30 × 30 cm), which prevented the participant from seeing their responses, but was low enough to permit them to view the computer screen. At a distance of 10 cm beyond the occluder was a standard computer keyboard; immediately beyond the keyboard was a manipulandum; and 30 cm beyond the manipulandum was a 17″ LCD computer screen. The manipulandum consisted of a wooden box (9 cm wide × 15 cm high × 5 cm deep) supported by two grey metal cylinders (each 7 cm high and 0.5 cm in diameter) on a flat wooden stand (21 cm wide × 12 cm deep; Figure 1). The front face of the wooden box was attached to the body of the box by four small springs, allowing it to be grasped in a power grip. The performance of a power grip on the body of the box resulted in the registration of a response by one of two buttons from a USB mouse contained within the manipulandum. Attached to the top of the wooden box was a flat piece of grey metal (5 cm high × 1 cm deep) bent into an inverted 'u' shape to form a 'clip' which could be grasped with a precision grip. The performance of a precision grip on the clip resulted in the registration of a response by the other USB mouse button contained within the manipulandum, which allowed the timing and identity of the performed grip to be recorded.

Action images, prepared using GNU Image Manipulation Program software (www.gimp.org), were presented in colour at a viewing distance of approximately 60 cm. In these images, the distance between the top and the bottom of the manipulandum subtended approximately 15 degrees of visual angle.

Procedure and stimuli. Participants performed a simple response time task with blocked responses. Between trials, the index finger of the participant's right hand rested on the spacebar of the computer keyboard. All trials began with presentation of a 'resting image' on the computer screen. The resting image showed the torso and arms of a 'model' actor in a black t-shirt, seated behind a table, with arms at rest on either side of a manipulandum (see Figure 1). The resting image was replaced after a variable duration (800, 1200, 1600, 2000 or 2400 ms) with a 'movement
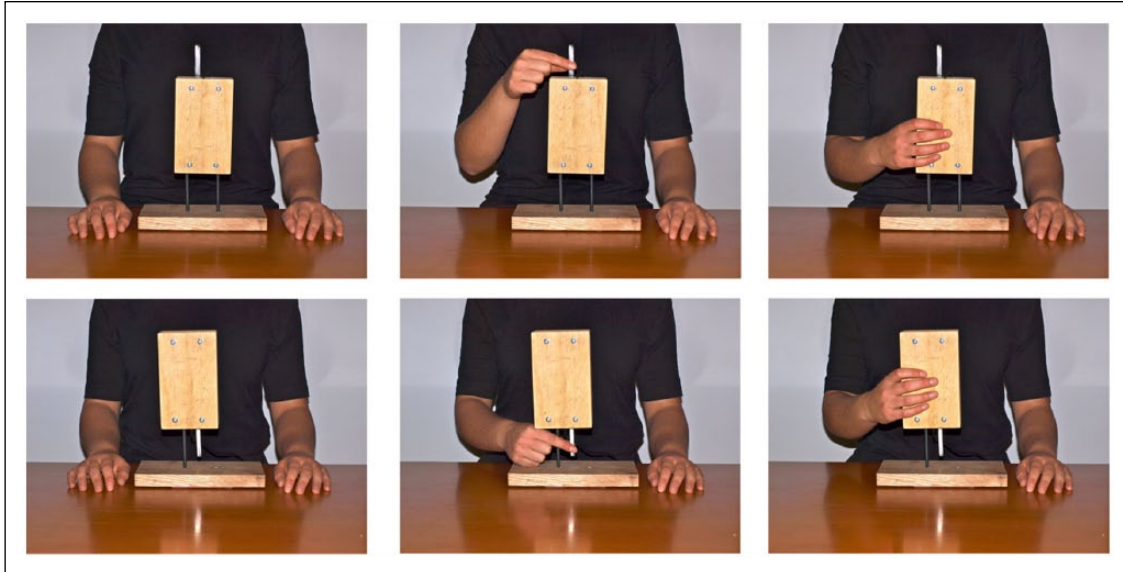
Figure 1. Resting (left) and movement (centre and right) images for each movement type (precision [centre] and power grip [right]) in each orientation (with the clip above [top row] or below [bottom row] the box). On trials where the correct response was a precision grip, the centre images are imitatively compatible, whereas the right images are imitatively incompatible, and since the participant performs a precision grip in the spatial location above the other response location, the top centre and bottom right images are spatially compatible, whereas the top right and bottom centre images are spatially incompatible. On trials where the correct response was a power grip, the centre images are imitatively incompatible, whereas the right images are imitatively compatible, and since the participant performs a power grip in the spatial location below the other response location, the top right and bottom centre images are spatially compatible, whereas the top centre and bottom right images are spatially incompatible.

image'. The movement image showed the model grasping the manipulandum. The participant was instructed to respond as quickly as possible to the onset of the movement image by releasing the computer key on which their finger had been resting and grasping the manipulandum with their right hand. The movement image remained on the screen until 1000 ms after the computer key had been released. A blank screen was then presented until the participant returned their finger to the spacebar, which triggered the onset of the following trial.

Participants were required to make the same response in every trial within a block – to pinch the clip on the manipulandum with the tips of their thumb and forefinger (precision grip) or to grasp the wooden box using their whole-hand (power grip). The form of the action performed by the model was technically task-irrelevant; participants were instructed to respond to the onset, not the content, of the movement image. Nonetheless, in half of the trials in any given block, the go signal (the movement image) was imitatively compatible; the movement image showed the model performing the same action (precision or power) that the participant had been instructed to perform in that block (precision stimulus–precision response, power stimulus–power response). In the other half of the trials, the go signal was imitatively incompatible; the movement image showed the model performing the alternative to the action that the participant had been instructed to perform in that block

(power stimulus–precision response, precision stimulus–power response). Furthermore, in half of the imitatively compatible and half of the imitatively incompatible trials, the go signal was spatially compatible, and in the other half, it was spatially incompatible. In spatially compatible trials, the resting and movement images showed the model acting on a manipulandum which was oriented such that the observed grip was in the same relative spatial location (above or below the other response location) as that in which participants made their response. For example, when participants were performing a precision response, this was performed in the response location above that for the power response, and thus, for spatially compatible trials with precision responses, the observed grip was also in the higher of the two response locations (meaning that when the observed grip was a precision grip, the manipulandum was in the same up-down orientation as the participant's manipulandum, with the clip at the top, whereas when the observed grip was a power grip, the manipulandum was inverted, with the clip at the bottom). For spatially compatible trials with power responses, the observed grip was in the lower part of the two response locations (meaning that when the observed grip was a power grip, the manipulandum was in the same up-down orientation as the participant's manipulandum, with the clip at the top, whereas when the observed grip was a precision grip, the manipulandum was inverted, with the clip at the bottom). In spatially incompatible trials,
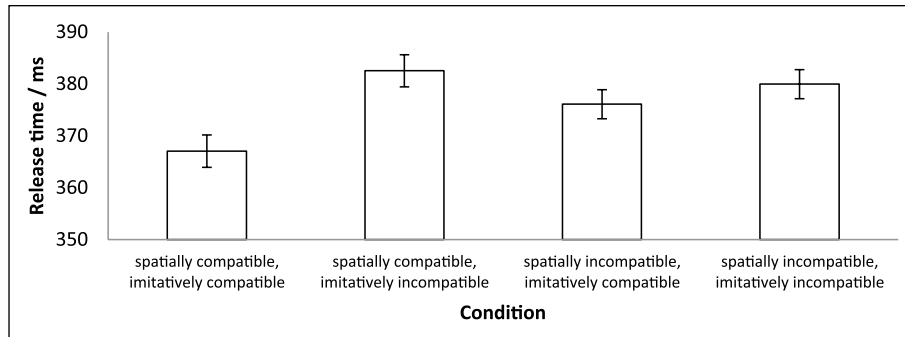
Figure 2. Mean release time for each of the four experimental conditions in Experiment 1. Error bars indicate standard error of the mean of the pairwise differences for the imitative compatibility effect at each level of spatial compatibility (Franz & Loftus, 2012).

the stimuli showed the model acting on a manipulandum which was oriented such that the observed grip was in the opposite relative spatial location (above or below the other response location) as that in which participants made their response. For example, for spatially incompatible trials with precision responses, the observed grip was in the lower part of the two response locations (meaning that when the observed grip was a precision grip, the manipulandum was inverted, with the clip at the bottom, whereas when the observed grip was a power grip, the manipulandum was in the same up-down orientation as the participant's manipulandum, with the clip at the top). For spatially incompatible trials with power responses, the observed grip was in the upper part of the two response locations (meaning that when the observed grip was a power grip, the manipulandum was inverted, with the clip at the bottom, whereas when the observed grip was a precision grip, the manipulandum was in the same up-down orientation as the participant's manipulandum, with the clip at the top). In other words, whereas participants' precision responses were always located above their power responses, when the model's manipulandum was inverted, the model's precision responses were located below their power responses, allowing the relative spatial location of the observed actions to be manipulated independently of the identity of the observed actions. Thus, in total, there were four experimental conditions comprising a factorial combination of imitative and spatial compatibility: imitatively compatible, spatially compatible (precision/above stimulus–precision/above response, power/below stimulus–power/below response); imitatively incompatible, spatially compatible (power/above stimulus–precision/above response, precision/below stimulus–power/below response); imitatively compatible, spatially incompatible (precision/below stimulus–precision/above response, power/above stimulus–power/below response); and imitatively incompatible, spatially incompatible (power/below stimulus–precision/above response, precision/above stimulus–power/below response).

A total of 160 experimental trials were presented across four blocks. The correct response for each block alternated in a counterbalanced order across participants, such that each participant completed two blocks in which precision responses were required and two blocks in which power responses were required. Trials of all four types (imitatively compatible, spatially compatible; imitatively incompatible, spatially compatible; imitatively compatible, spatially incompatible; imitatively incompatible, spatially incompatible) were presented in random order in each block. Across blocks, there were 40 trials of each type. In addition to the 40 experimental trials in each block, there were 10 trials per block in which the stimulus hand did not move and instead the resting image was presented for 3000 ms. These 'catch' trials ensured that participants did not respond until they observed a movement. Each block was preceded by five practice trials comprising one trial of each type and a catch trial.

For each trial, release time was measured from the onset of the movement image until the participant released the spacebar. Movement time was measured from the time at which the participant released the spacebar until the participant grasped the manipulandum. Previous effects of imitative compatibility on response times to perform goal-directed actions have been found in the release time component of the response (Newman-Norlund et al., 2010), and therefore this was where we also expected to observe effects.

Results

Error trials (i.e., performing a movement on a catch trial or making an incorrect response, e.g., power grip during a precision grip block) were removed from the data set, along with outlying trials on which the participant's response was more than 2.5 *SD* from their mean response for that variable (i.e., release or movement time). Mean release time and movement time were then calculated for each of the four conditions, along with error rates.

Release time. The release time data for each of the four conditions are displayed in Figure 2. It can be seen that

Table 1. Movement time data (ms) for imitation test sessions in Experiments 1 and 2.

	Spatially compatible, imitatively compatible		Spatially compatible, imitatively incompatible		Spatially incompatible, imitatively compatible		Spatially incompatible, imitatively incompatible	
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
Experiment 1	559.8	21.5	560.1	22.9	553.4	21.7	559.6	21.2
Experiment 2: pre-training, mirror group	600.9	35.8	601.4	35.2	604.8	34.7	609.4	36.1
Experiment 2: pre-training, counter-mirror group	570.5	30.8	564.7	31.8	575.4	31.6	574.4	31.7
Experiment 2: post-training, mirror group	542.0	37.6	539.2	36.4	542.3	36.9	543.7	38.3
Experiment 2: post-training, counter-mirror group	543.1	32.9	543.5	32.9	546.0	32.4	541.0	30.9

SEM: standard error of the mean.

Table 2. Error rate data (%) for experimental trials in imitation test sessions in Experiments 1 and 2.

	Spatially compatible, imitatively compatible		Spatially compatible, imitatively incompatible		Spatially incompatible, imitatively compatible		Spatially incompatible, imitatively incompatible	
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
Experiment 1	1.1	0.5	1.7	0.9	3.0	1.4	1.9	0.6
Experiment 2: pre-training, mirror group	1.1	0.3	1.3	0.2	0.8	0.3	1.5	0.5
Experiment 2: pre-training, counter-mirror group	0.9	0.2	1.3	0.4	1.2	0.2	1.3	0.4
Experiment 2: post-training, mirror group	0.8	0.4	0.7	0.3	1.1	0.5	1.0	0.5
Experiment 2: post-training, counter-mirror group	1.0	0.4	0.9	0.3	0.4	0.2	0.9	0.3

SEM: standard error of the mean.

although participants were faster to perform an imitatively compatible than incompatible response, this effect appeared to be modulated by spatial compatibility, being smaller for spatially incompatible trials. The release time data were subjected to analysis of variance (ANOVA) with within-subjects factors of imitative compatibility (compatible, incompatible) and spatial compatibility (compatible, incompatible). A main effect of imitative compatibility was observed, $F(1, 15) = 6.84$, $p = 0.020$, $\eta_p^2 = 0.313$, magnitude $= 9.7 \pm 3.7$ ms (mean $\pm$ standard error of the mean [*SEM*]), indicating that release times were faster on imitatively compatible than incompatible trials; however, this was modulated by an interaction between spatial and imitative compatibility, $F(1, 15) = 9.11$, $p = 0.009$, $\eta_p^2 = 0.378$. Follow-up tests of the simple effect of imitative compatibility at each level of spatial compatibility revealed that the imitative compatibility effect was significant on spatially compatible trials, $F(1, 15) = 12.46$, $p = 0.003$, $\eta_p^2 = 0.454$, magnitude $= 15.5 \pm 4.4$ ms, but not on spatially incompatible trials, $F(1, 15) = 0.96$, $p = 0.342$, $\eta_p^2 = 0.060$, magnitude $= 3.9 \pm 3.9$ ms).

Movement time. As found in previous studies of goal-directed imitation (Newman-Norlund et al., 2010), movement time did not differ markedly between conditions (see Table 1). These data were subjected to the same ANOVA as that for release time, and no significant effects were found. Detection of effects on release time but not on movement time suggests that the spatial and imitative properties of observed actions modulate processes involved in response preparation rather than response execution.

Errors. Error rates did not differ markedly between conditions (see Table 2).

Response type analysis. Three further analyses were performed on the release time, movement time and error rate data, including an additional factor of response type (precision grip, power grip) in the ANOVA described above. The performance of a precision grip resulted in slower release and movement times, and more errors, than the performance of a power grip (release time: $F(1, 15) = 23.02$, $p < 0.001$, $\eta_p^2 = 0.606$; movement time: $F(1, 15) = 45.37$, $p < 0.001$, $\eta_p^2 = 0.752$; error rate: $F(1, 15) = 5.80$, $p = 0.029$, $\eta_p^2 = 0.279$). For release times, there was an interaction between spatial compatibility and response type, such that the effect of spatial compatibility was greater on trials requiring a precision grip response than on trials requiring a power grip response, $F(1, 15) = 14.70$, $p = 0.002$, $\eta_p^2 = 0.495$. Response type did not interact with any other factor, and the inclusion of response type in the analyses did not affect any of the effects reported above; therefore, these data were not analysed further and response type was not included as a factor in subsequent analyses.

Discussion

Previous experiments examining the imitation of goal-directed actions have typically confounded imitative compatibility (the tendency to respond more quickly when performing an action with the same, rather than different, spatial relations among parts of the body) with spatial compatibility (the tendency to respond more quickly when performing a response at the same, rather than a different, location). Experiment 1 sought to determine whether effects of imitative compatibility on response times could be measured when controlling for spatial compatibility by including two additional trial types in which imitative and spatial compatibility were in opposition. This allowed us to cross the factors of imitative and spatial compatibility and thus to isolate the effect of imitative compatibility on response times.

We observed an interaction between the factors of imitative and spatial compatibility, such that the effect of imitative compatibility was only present on spatially compatible trials. This may be an attentional effect. That is, participants may pay more attention to the topography of an observed body movement when it occurs at a location to which they are planning to make a response than when the observed movement occurs at a spatially distinct location (Press, Gherri, Heyes, & Eimer, 2010; Rizzolatti, Riggio, Dascola, & Umiltá, 1987). Whatever the mechanism, this result demonstrates the need to control for spatial compatibility when measuring imitation of goal-directed actions and provides a method by which imitative compatibility can be measured while controlling for spatial compatibility.

Experiment 2 therefore used the method of Experiment 1 to measure imitation of goal-directed actions before and after a period of sensorimotor learning to establish whether associative learning can modulate imitation of goal-directed actions.

Experiment 2

Having shown in Experiment 1 that it is possible to measure imitative compatibility for goal-directed actions when spatial compatibility is controlled, Experiment 2 investigated the effect of sensorimotor training on imitative compatibility for goal-directed actions. Participants performed the same simple response time task as in Experiment 1 on two occasions: before and 24 hr after a period of sensorimotor training. Participants were randomly assigned to one of two training groups, receiving either 'counter-mirror' or 'mirror' sensorimotor training. In every training trial, participants in the counter-mirror group performed the opposite action to that which they observed (i.e., performed a precision grip when they observed a power grip, and vice versa). The ASL model suggests that this training establishes new excitatory and/or inhibitory links between action representations – for example, an excitatory association between the sight of a power grip and the performance of a precision grip, and an inhibitory link between the sight of power grip and the performance of power grip. If the capacity to imitate arises as a result of associative learning, then during the subsequent imitation test, the sight of a power grip should activate the motor programme for precision grip instead of the programme for power grip, leading to a reduced or abolished imitative compatibility effect after counter-mirror sensorimotor training. Participants in the mirror group, in contrast, received training in which, on every trial, they performed the same action as that which they observed, providing them with experience equivalent to that received during a lifetime of observing their own actions. The inclusion of the mirror training group, in which participants perform and observe the two actions the same number of times as participants in the counter-mirror group, controls for the possibility that any effects of training seen in the counter-mirror group are due purely to sensory experience of observing the two actions or purely to motor experience of performing the two actions.

Method

Participants. In total, 36 new participants were recruited via the University of Surrey experiment participation pool and randomly allocated to either the counter-mirror or mirror training group. Four participants were replacements for those who made more than 15% errors on either experimental or catch trials in either the pre- or post-training test session; thus, the final sample comprised 32 participants

(seven males) aged 18-32 years (mean = 21.5 years, SD = 3.6), with 16 participants randomly assigned to each training group. Participants received course credit or a small honorarium for their time. Experimental procedures were approved by the University of Surrey Ethics Committee and followed the Declaration of Helsinki.

Procedure

Pre- and post-training test sessions. These were identical to Experiment 1. The pre-training test session took place about 10 days before the training session (mean = 9.9 days, SEM = 1.3). The two groups did not differ in the interval between the pre-training test session and training session, $t(30) = 0.05$, $p = 0.963$, $d = 0.014$. The training session took place 24 hr before the post-training test session.

Training. Participants performed 400 training trials over 10 blocks. On half of the trials, the observed movement was a precision grip, and on the other half, it was a power grip. Participants in the mirror training group were instructed to perform the same grip as that which they observed, whereas participants in the counter-mirror training group were instructed to perform the other grip (precision grip when they observed a power grip, and vice versa). No catch trials were included during training.

Observed movements were presented in a random order with 20 of each movement type per block. Both orientations of the observed manipulandum were included among the training stimuli, distributed evenly across movement types; thus, participants performed both spatially compatible and spatially incompatible responses during training, regardless of their training group. The trial timings were identical to those in Experiment 1.

Results.

The data were processed and analysed as for Experiment 1.

Training. Due to a technical error, the data from one participant were not recorded during training. Error rates were low (mean < 1%) and did not differ between groups (mean ± SEM, mirror training group = 0.9 ± 0.1%; counter-mirror training group = 1.1 ± 0.2%; $t(29) = 0.46$, $p = 0.651$, $d = 0.14$).

Figure 3 displays the release time data for each training group across training blocks. The release time data were subjected to ANOVA with within-subjects factor of training block (1-10) and between-subjects factor of training type (mirror, counter-mirror). A trend towards a main effect of block was found, $F(9, 261) = 1.78$, $p = 0.073$, $\eta_p^2 = 0.058$, indicating that release times reduced over the course of training. A follow-up analysis confirmed that release times were faster in the final training block (438 ± 17 ms) than in the first training block (466 ± 16 ms; $t(30) = 2.09$, $p = 0.045$, $d = 0.29$). No main effect of training type, or interaction between block and training type, was found.

The movement time data (mean ± SEM, 647 ± 25 ms) were subjected to the same ANOVA, and no main effects or interactions were found.

Pre- and post-training. Error rates were low (mean for both experimental and catch trials for both sessions <3%; see Table 2).
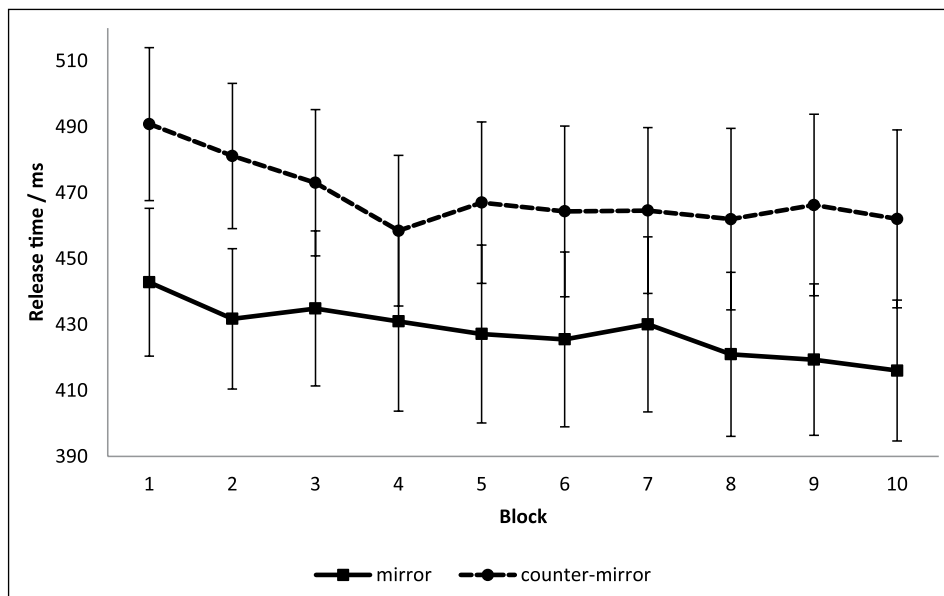

Figure 3. Mean release time during training in Experiment 2 for each training group. Error bars indicate (traditional, between-subjects) standard error of the mean.

Release time. Figure 4 displays the release time data for each training group for each condition within each test session. The release time data were subjected to ANOVA with within-subjects factors of session (pre-training, post-training), spatial compatibility (compatible, incompatible) and imitative compatibility (compatible, incompatible), and between-subjects factor of training type (mirror, counter-mirror). A main effect of imitative compatibility was observed, $F(1, 30)=8.29$, $p=0.007$, $\eta_p^2 = 0.216$, magnitude$=5.2\pm1.8$ ms, indicating that release times were faster on imitatively compatible than imitatively incompatible trials; however, replicating the results of Experiment 1, this was modulated by an interaction between spatial and imitative compatibility, $F(1, 30)=18.83$, $p<0.001$, $\eta_p^2 = 0.386$, driven by a larger imitative compatibility effect on spatially compatible trials (magnitude$=11.6\pm2.7$ ms) than on spatially incompatible trials (magnitude$=-1.2\pm1.9$ ms). Crucially, there was a three-way interaction between imitative compatibility, session and training type, $F(1, 30)=4.57$, $p=0.041$, $\eta_p^2 = 0.132$. No other main effects or interactions reached significance.

Follow-up analysis indicated that the imitative compatibility effect was significantly reduced in the counter-mirror training group in the post-training session compared to the pre-training session (simple interaction between imitative compatibility and session in the counter-mirror training group: $F(1, 15)=7.28$, $p=0.016$, $\eta_p^2 = 0.327$), with a significant imitative compatibility effect in the pre-training session, $F(1, 15)=11.45$, $p=0.004$, $\eta_p^2 = 0.433$, magnitude$=11.8\pm3.5$ ms, but not in the post-training session, $F(1, 15)=0.19$, $p=0.673$, $\eta_p^2 = 0.012$, magnitude$=0.8\pm1.8$ ms. In contrast, in the mirror training group, the magnitude of the imitative compatibility effect was not significantly altered as a result of training (simple interaction between imitative compatibility and session in the mirror training group: $F(1, 15)=0.777$, $p=0.392$, $\eta_p^2 = 0.049$.

Movement time. The movement time data (Table 1) were subjected to the same ANOVA as that for release time. A main effect of session was observed, $F(1, 30)=17.38$, $p<0.001$, $\eta_p^2 = 0.367$, with movement times being signif-
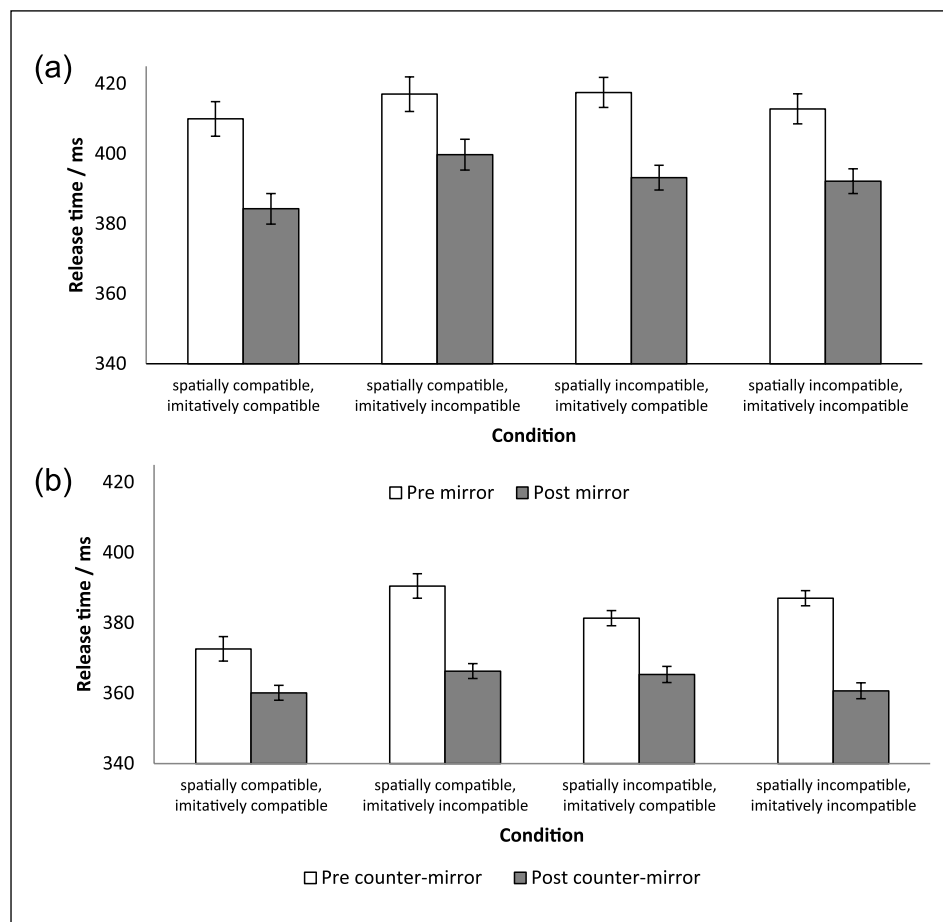

Figure 4. Mean release time in Experiment 2 for (a) the mirror training group and (b) the counter-mirror training group. Error bars indicate standard error of the mean of the pairwise differences for the imitative compatibility effect at each level of spatial compatibility within each session in each group.

icantly faster in the post-training (543 ± 25 ms) than in the pre-training (588 ± 24 ms) session. An interaction between spatial and imitative compatibility was also observed, $F(1, 30) = 8.11$, $p = 0.008$, $\eta_p^2 = 0.213$, driven by a larger imitative compatibility effect on spatially compatible trials (magnitude = 3.0 ± 2.0 ms) than on spatially incompatible trials (magnitude = -4.9 ± 1.9 ms); however, given that this effect did not interact with session or training type, these data were not analysed further. No other main effects or interactions reached significance.

Discussion

Experiment 2 sought to determine whether sensorimotor learning can modulate imitation of goal-directed actions. We found a three-way interaction between the effects of imitative compatibility, testing session and training type on release times, indicating that counter-mirror training selectively abolished imitation of goal-directed actions; an imitative compatibility effect was detected before but not after training in which the sight of one action was systematically paired with the performance of a different action. Counter-mirror training did not change the magnitude of the spatial compatibility effect. Furthermore, abolition of the imitative compatibility effect did not occur in the mirror training group, suggesting that the counter-mirror training reduced imitation, not by providing participants with additional experience of seeing and/or doing the grasping actions but via sensorimotor learning – by forging new associations between sensory and motor representations.

General discussion

Experiment 1 demonstrated that it is possible to isolate the effects of imitative compatibility from those of spatial compatibility when measuring imitation of goal-directed actions. Experiment 2 built on this result by showing that counter-mirror training, in which the sight of an action is paired with performance of a topographically nonmatching action, suppresses imitation of goal-directed actions but not the tendency to respond in a spatially compatible manner to the observation of such actions.

By demonstrating that imitation of goal-directed actions is affected by sensorimotor training in the same way that has previously been shown for intransitive actions (Cook et al., 2012; Cook et al., 2010; Gillmeister et al., 2008; Heyes et al., 2005; Press et al., 2007; Wiggett et al., 2011), the results of these experiments provide strong support for the view that associative learning mechanisms underlie the development of the capacity for imitation. Specifically, they suggest that a relatively short period of associative learning is sufficient to set up new excitatory and/or inhibitory associations between sensory and motor representations of action which abolish the behavioural tendency to imitate the trained action. The

fact that this result has been found for goal-directed actions provides stronger evidence than was previously available in support of the view that the same associative mechanisms underlie the development of the matching properties of mirror neurons (the putative neural substrate of the capacity to imitate; Catmur et al., 2009; Heiser, Iacoboni, Maeda, Marcus, & Mazziotta, 2003; Newman-Norlund et al., 2010). It is claimed that these neurons preferentially encode goal-directed actions (Gallese et al., 1996; Rizzolatti & Fogassi, 2014; Rizzolatti & Sinigaglia, 2010), and previous sensorimotor training experiments have been criticised on the grounds that they did not test imitation of, or mirror neuronal responses to, goal-directed actions (Rizzolatti & Sinigaglia, 2010).

It has been suggested that the effects of sensorimotor training on imitation and mirror neuron responses could arise, not via associative mechanisms but instead as a result of rule-based cognitive strategies (Barchiesi & Cattaneo, 2013; Bardi, Bundt, Notebaert, & Brass, 2015; Ubaldi, Barchiesi, & Cattaneo, 2015). For example, rather than forming excitatory associations between sensory and motor representations of different actions and/or inhibitory associations between sensory and motor representations of the same actions, participants in the counter-mirror training group might learn the rule 'do opposite' during training and then implement this rule at post-test such that response times are speeded on incompatible trials and/or slowed on compatible trials. Experiments purporting to favour a rule-based account have two weaknesses. First, they have not shown that, without training of a kind that would support associative learning, a counter-mirror instruction is sufficient to reduce or abolish an imitative compatibility effect. For example, Bardi et al. (2015) found a smaller imitative compatibility effect following a treatment in which participants were exposed to a succession of movement stimuli and encouraged, by the preliminary instructions, to imagine themselves performing the opposite action in response to each stimulus, i.e., following a treatment that would be expected to support associative learning. Second, in Experiments 1 and 2, and in previous studies testing the associative account, there was a 24-hr interval between counter-mirror training and the post-test, but in studies purporting to favour a rule-based account, the post-test has immediately followed the counter-mirror treatment. Thus, even if we assume that, in those studies, the counter-mirror treatment reduced the imitative compatibility effect via a rule-based rather than an associative route, those studies do not show that a rule, rather than associative learning, is responsible when there is a substantial delay before testing. Research on task switching indicates the instructions or response set for an earlier task can interfere with performance on a subsequent task, but that this effect reduces when the interval between the two tasks increases to over 1 s and that it does not persist beyond the initial trial of the second task (e.g., Rogers & Monsell, 1995). It therefore

seems unlikely that the response set for an earlier task could interfere with subsequent task performance when there is a 24-hr interval between the tasks, as in the present case.

The finding, in Experiment 2, that counter-mirror training affected imitative but not spatial compatibility provides an additional reason to doubt that counter-mirror training has its effects via rule-based cognitive strategies. If participants in the counter-mirror training group were merely implementing the rule 'do opposite' at post-test, then, compared with the mirror training group, one would expect them to have shown smaller imitative and spatial compatibility effects after training. In principle, the counter-mirror group could have learned and implemented the rule 'do opposite when spatially compatible', but it is not clear on what basis they might have formulated this rule, given that the training instructions did not refer to spatial compatibility, half of the training trials were spatially incompatible and, in these trials as in all others, participants in the counter-mirror group were required to 'do opposite'. Similarly, in principle, the counter-mirror group could have learned during training the rule 'do opposite grip', but again we do not know of any evidence that previous task instructions or rules can influence performance on a subsequent task following a 24-hr delay. In addition, it is not clear why participants would have persisted in applying this or any other rule on test when it interfered with discharging task instructions by retarding responses in compatible trials. It is known that 'logical recoding' (Hedge & Marsh, 1975) can result in participants who have been instructed to make incompatible responses on one stimulus dimension responding more slowly in trials that are compatible with respect to another, simultaneously presented stimulus dimension. For example, when participants responding to red and green lights by pressing a left key coloured red and a right key coloured green are told to respond to the red light with the green key and the green light with the red key, response times on spatially compatible trials are longer than on spatially incompatible trials (Hedge & Marsh, 1975). However, as far as we are aware, there is no evidence that this kind of interference effect, based on rule transfer, can occur across successive tasks (and in this case, successive days) rather than across stimulus dimensions.

In supporting the ASL model of imitation, the current data add to a growing literature suggesting that phylogenetically ancient mechanisms of associative learning underlie the development and online control of abilities that are crucial for human social interaction (Behrens, Hunt, Woolrich, & Rushworth, 2008; Frith & Frith, 2012; Heyes, 2016). Given that our understanding of associative learning is based predominantly on experiments with non-human animals, this trend is part of a 'return swing of the pendulum in the often uneasy relationship between experimental psychologists studying human perception, learning, memory and cognition, and those who study the

behavior of other animals' (Mackintosh, 1994, p. xvii). As Mackintosh showed, through argument and shining example, one can both rejoice in the passing of behaviourism and find deep explanations for human behaviour in research on conditioning and associative learning in animals (Mackintosh, 1974, 1983).

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