Contextual Modulation of Mirror and Countermirror Sensorimotor Associations

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Automatic imitation—the unintended copying of observed actions—is thought to be a behavioral product of the mirror neuron system (MNS). Evidence that the MNS develops through associative learning comes from previous research showing that automatic imitation is attenuated by countermirror training, in which the observation of one action is paired contingently with the execution of a different action. If the associative account of the MNS is correct, countermirror training should show context specificity, because countermirror associations render action stimuli ambiguous, and ambiguity promotes contextual control. Two experiments that confirm this prediction are reported. In Experiment 1 we found less residual automatic imitation when human participants were tested in their countermirror training context. In Experiment 2, sensorimotor training where participants made action responses to novel abstract stimuli was insensitive to the same context manipulation, confirming that the former result was not a procedural artifact. Contextual modulation may enable the MNS to function effectively in spite of the fact that action observation often excites multiple conflicting MNS responses.

Keywords: automatic imitation, associative sequence learning, mirror neuron system, context, countermirror training

Mirror neurons (MNs) are commonly characterized as single neurons that respond selectively during both the observation and execution of the same action—for example, to the observation and performance of a precision grip but not during the observation or performance of a power grip. However, a close reading of the results from single-cell recording indicates that substantial proportions of macaque MNs (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Ferrari, Gallese, Rizzolatti, & Fogassi, 2003; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rozzi, Ferrari, Bonini, Rizzolatti, & Fogassi, 2008; Umiltà et al., 2001) and human sensorimotor units (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010) discharge indiscriminately during the observation of multiple actions or selectively during the observation and execution of different actions. These findings suggest that the sight of an action may often excite several different congruent and noncongruent motor representations. Such conflicting MN responses are

potentially problematic for accounts that propose that the MNS mediates action understanding (Rizzolatti & Craighero, 2004; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996), imitation (Heyes, 2001, 2011; Iacoboni, 2009), or generic action selection (Hickok & Hauser, 2010). However, through its appeal to the principles of associative learning to explain the development of MNs, the associative sequence learning (ASL) model (Heyes, 2001, 2010a, 2010b; Ray & Heyes, 2011) suggests that contextual modulation may enable the mirror neuron system (MNS) to function effectively in spite of the conflicting responses of individual MNs. To investigate whether the MNS is subject to contextual modulation, the present study examined the effects of context on automatic imitation—a behavioral effect widely thought to be mediated by the human MNS.

Automatic Imitation and the Mirror Neuron System

Automatic imitation is a robust behavioral effect in which the topographical features of task-irrelevant action stimuli facilitate similar, and interfere with dissimilar, motor responses (Brass, Bekkering, & Prinz, 2001; Heyes, Bird, Johnson, & Haggard, 2005; Stürmer, Aschersleben, & Prinz, 2000). For example, participants are faster to make hand-open responses to the onset of hand-opening stimuli than to the onset of hand-closing stimuli (Heyes et al., 2005). Similarly, participants execute finger lift responses faster to the onset of finger-lifting stimuli than to the onset of finger-tapping stimuli (Brass et al., 2001). The finding that participants make faster imitative responses than nonimitative responses is highly robust (Heyes, 2011), having been reported for

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several effector systems (Gillmeister, Catmur, Liepelt, Brass, & Heyes, 2008; Leighton & Heyes, 2010) and for both transitive (Craighero, Bello, Fadiga, & Rizzolatti, 2002) and intransitive (Press, Bird, Walsh, & Heyes, 2008) actions. Moreover, studies have confirmed that this effect is truly imitative; it depends on the topography of observed actions—on how body parts move relative to one another—not merely on spatial compatibility, the position of the action relative to an external frame of reference (Catmur & Heyes, 2010; Cooper, Catmur, & Heyes, in press).

It is likely that automatic imitation is mediated by the same processes as are motor mimicry and mirror effects (Heyes, 2011; Wang, Newport, & Hamilton, 2011). The term *motor mimicry* is used to describe the occurrence of spontaneous, unconscious imitation in naturalistic social settings (Chartrand & Bargh, 1999; Cook, Bird, Lunser, Huck, & Heyes, 2011). For example, participants are more likely to engage in foot-tapping than face-touching behaviors in the presence of foot-tapping confederates, while the opposite pattern is observed in the presence of confederates prone to touching their face (Chartrand & Bargh, 1999). *Mirror effects* provide evidence of covert imitation within the human motor system (Dimberg, Thunberg, & Elmehed, 2000; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Strafella & Paus, 2000). For example, during passive observation of actions, motor-evoked potentials (MEPs) recorded from the muscles involved in performing the observed action are greater than MEPs recorded from task-irrelevant muscles (Fadiga et al., 1995; Strafella & Paus, 2000).

Automatic imitation is widely thought to be a product of a human MNS (Bien, Roebroeck, Goebel, & Sack, 2009; Blakemore & Frith, 2005; Catmur, Walsh, & Heyes, 2009; Ferrari, Bonini, & Fogassi, 2009; Heyes, 2011; Iacoboni, 2009; Longo, Kosobud, & Bertenthal, 2008; Rizzolatti, Fogassi, & Gallese, 2001). MNs are single units identified in the ventral premotor (area F5) and inferior parietal (area PF) cortices of the macaque (di Pellegrino et al., 1992; Fogassi et al., 2005; Gallese et al., 1996; Rizzolatti et al., 1996), which respond to both the sight and execution of transitive and communicative actions. Since the discovery of MNs in monkeys, considerable indirect evidence has accumulated suggesting that humans also have an MNS. Numerous neuroimaging studies have revealed premotor and parietal areas of the human brain that respond to the observation and execution of transitive and intransitive actions (Buccino et al., 2001; Chong, Cunnington, Williams, Kanwisher, & Mattingley, 2008; Fadiga et al., 1995; Gazzola, Rizzolatti, Wicker, & Keysers, 2007; Grèzes, Armony, Rowe, & Passingham, 2003; Iacoboni et al., 1999; Kilner, Neal, Weiskopf, Friston, & Frith, 2009). Single-cell recording in patients with intractable epilepsy has also identified neurons with mirror properties in the medial wall (supplementary motor area, cingulate cortex) and the medial temporal lobe (hippocampus, parahippocampal gyrus, entorhinal cortex, and amygdala) of the human brain (Mukamel et al., 2010). Although some studies have failed to find evidence of a human MNS (Dinstein, Gardner, Jazayeri, & Heeger, 2008; Lingnau, Gesierich, & Caramazza, 2009), the balance of evidence provides clear support for the existence of such a network (Molenberghs, Cunnington, & Mattingley, 2009, 2011; Morin & Grèzes, 2008).

Evidence from functional magnetic resonance imaging (fMRI) paradigms suggests that the MNS mediates automatic imitation. For example, sensorimotor training that modulates the magnitude of participants' automatic imitation effects also modulates the magnitude of the blood oxygen level dependent (BOLD) response in premotor areas thought to be part of the MNS (Catmur et al., 2008). Convergent evidence has also been derived using transcranial magnetic stimulation (TMS). Specifically, the application of disruptive TMS to the inferior frontal gyrus (IFG) has been shown to abolish the automatic imitation effect (Catmur et al., 2009; Heiser, Iacoboni, Maeda, Marcus, & Mazziotta, 2003; Newman-Norlund, Ondobaka, van Schie, van Elswijk, & Bekkering, 2010). The IFG is thought to be the human homologue of the macaque premotor region F5 and is widely regarded as a key component of the human MNS (Kilner et al., 2009). Reports that virtual lesions to this area abolish automatic imitation are therefore important because they suggest that the MNS, and the IFG in particular, makes a necessary causal contribution to this effect.

MNs are frequently characterized as neurons that respond selectively to the observation and execution of the same action (Arnstein, Cui, Keysers, Maurits, & Gazzola, 2011; Chong et al., 2008; Dinstein, Hasson, Rubin, & Heeger, 2007; Dinstein, Thomas, Behrmann, & Heeger, 2008; Keysers & Gazzola, 2010). However, a surprising number of MNs do not exhibit sensorimotor congruency. The few studies of macaque MNs that have reported detailed congruency analyses all describe substantial proportions (6%–30%) of so-called noncongruent (or "logically related") MNs that respond to the observation and execution of different actions (di Pellegrino et al., 1992; Gallese et al., 1996; Rozzi et al., 2008). In addition, they indicate that a significant proportion of macaque MNs (15%–65%) are "ambiguous" in that they respond to the observation or execution of multiple actions (di Pellegrino et al., 1992; Ferrari et al., 2003; Gallese et al., 1996; Rozzi et al., 2008; Umiltà et al., 2001). Similarly, the study of sensorimotor units in human participants has revealed large proportions of neurons with both noncongruent and ambiguous sensorimotor properties (Mukamel et al., 2010).

Ontogenetic Origins of the Mirror Neuron System

Considerable evidence has accumulated indicating that learning plays a crucial role in the development of the human MNS. Neuroimaging studies of sensorimotor expertise have taken advantage of naturally occurring variation in participants' sensorimotor experience to better understand how learning shapes the motor responses elicited by action observation. For example, during the observation of finger movements in expert pianists but not in nonpianist controls, the fMRI BOLD response in premotor areas is stronger for movements that are piano-related than for those that are arbitrary (Haslinger et al., 2005). Similarly, capoeira and ballet dancers show stronger motor responses when viewing sequences of dance movements from their own genre (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005). Using a similar design, it has also been reported that male and female ballet dancers show greater motor activation when viewing dance sequences unique to their gender (Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006). Because dancers had equivalent visual exposure to the movements of both sexes, this finding cannot be attributed to visual experience alone.

"Countermirror" training studies have suggested not only that learning plays a crucial role in the ontogeny of the MNS but more specifically that its development is driven by associative learning based on sensorimotor experience. The logic behind these training

studies is simple: If the MNS develops through associative learning, then markers of MNS activity should be reduced or even reversed by training in which the execution of one action is contingent upon the observation of a different action. The first countermirror training study was reported by Heyes et al. (2005). Participants in the countermirror group first completed a training session during which they repeatedly made hand-open responses to hand-close stimuli and hand-close responses to hand-open stimuli. When tested 24 hr later, the countermirror group showed much smaller residual automatic imitation effects than did a mirror control group trained to execute imitative responses. Countermirror training has since been shown to reverse the mirror pattern of MEPs seen during action observation (Catmur, Mars, Rushworth, & Heyes, 2010; Catmur, Walsh, & Heyes, 2007) and to modulate the BOLD response in fMRI studies of the human MNS (Catmur et al., 2008). By showing that countermirror training has parallel effects on behavioral responses (automatic imitation) and on electrophysical and neuroimaging markers of MNS function, these studies have provided convergent evidence that the MNS mediates automatic imitation and that countermirror learning serves to modulate the activity of MNs.

The countermirror training paradigm was developed to test the ASL model of the origins of the MNS. This model proposes that MNs are a product of the same domain-general mechanisms of associative learning that produce Pavlovian and instrumental conditioning phenomena in humans and animals (Brass & Heyes, 2005; Heyes, 2001, 2010a, 2010b; Ray & Heyes, 2011). Where the observation of an action is contingent on the execution of an action, or vice versa, ASL posits that the respective visual and motor representations will become associated. It is these associations that are thought to endow MNs with their sensorimotor properties. Many of the sensorimotor contingencies one experiences are matching, where observed and executed actions correspond and therefore give rise to congruent MNs and automatic imitation. Experience of this kind is provided by, for example, visual monitoring of one's own actions, synchronous activity in response to a common stimulus, and being imitated by others (Ray & Heyes, 2011). However, exposure to nonmatching sensorimotor contingencies may cause the emergence of noncongruent MNs through the same learning mechanisms (Cook, Press, Dickinson, & Heyes, 2010). Similarly, where the sight of an action predicts the execution of more than one action, or where action execution predicts the observation of several actions, ambiguous MNs may emerge with multiple effective actions.

Ambiguity and Context

The sensorimotor properties of ambiguous and noncongruent MNs suggest that observing a given action often excites several different motor representations. This ambiguity is problematic for accounts that propose that the MNS makes a functional contribution to action understanding (Rizzolatti & Craighero, 2004; Rizzolatti et al., 1996), imitation (Heyes, 2001, 2011; Iacoboni, 2009), or generic action selection (Hickok & Hauser, 2010), because it implies uncertainty about how observed actions should be "understood" or which responses "selected." The conflicting motor representations excited by congruent and noncongruent MNs makes it unclear which interpretation or response is appropriate in a given situation. The associative account of MNS development, embodied

in the ASL model, suggests a potential mechanism for resolving the ambiguity caused by conflicting MN responses. Associative learning theory suggests that where a stimulus is rendered ambiguous by virtue of being associated with multiple outcomes, the ambiguity is resolved through contextual modulation. While the first associations formed with a novel stimulus generalize well to other contexts, subsequently acquired associations, which give rise to ambiguity, demonstrate greater contextual specificity (Bouton, 1993, 1994; Nelson, 2002).

Understanding of contextual modulation has been advanced by the study of two related conditioning effects: renewal and counterconditioning. In renewal designs, participants are first placed in Context A, where they learn that a stimulus predicts a certain outcome. Once the initial association has been acquired, participants are transferred to Context B, where they learn that the same stimulus no longer predicts that outcome. However, the extinction learning that takes place during this second phase is subject to contextual control: When transferred back to Context A (ABA renewal) or placed in a novel Context C (ABC renewal), a renewal of responding occurs (i.e., participants exhibit the conditioned response acquired during the first phase; Bouton & King, 1983; Nelson, Sanjuan Mdel, Vadillo-Ruiz, Perez, & Leon, 2011). In these studies, *context* typically refers to the physical environment provided by the conditioning chamber or testing cubicle. However the definition of *context* may be extended to include internal states, such as those induced by the presence of alcohol or a tranquilizer (Bouton, 1993, 1994).

Of more direct relevance to countermirror training are demonstrations that stimulus ambiguity plays a similar role in the contextual control of counterconditioning. Counterconditioning is an associative learning paradigm in which the conditioned responses to a stimulus vary across successive phases of a training procedure. Typically participants are first placed on a training schedule where they learn that a stimulus signals one outcome before being placed on a second conditioning schedule in which the same stimulus predicts a different outcome. Importantly, the asymmetric learning seen in renewal is also observed in counterconditioning. While the conditioned response acquired in the first phase is relatively insensitive to changes in context, the learning that occurs in the second phase is often far more context-specific. For example, Peck and Bouton (1990) initially trained rats to expect a mild electric shock following a tone in Context A before transferring them to a second schedule, where the tone signaled the delivery of food in Context B. Although the original conditioned response was reduced during training in Context B, it reemerged when the rats were returned to Context A or placed in a novel Context C.

The Present Study

The aim of the present study was to test the hypothesis, advanced by the ASL model, that when the sight of an action is associated with rival mirror and countermirror responses, the resulting ambiguity is resolved through contextual modulation. Applying the terminology used in studies of counterconditioning and renewal, ASL implies that the congruent MNs responsible for automatic imitation are a product of first-learned "mirror" associations. Each of these associations connects a sensory representation of an action with a motor representation of the same action and is acquired through everyday experience of a predictive rela-

tionship between the observation and execution of the same actions. The ASL model further implies that, during countermirror training, participants acquire a set of second-learned "countermirror" associations, connecting sensory representations of actions with motor representation of different actions. Therefore, if the ASL model is correct in suggesting that MNS development and modification depend on associative learning, then countermirror learning, like counterconditioning, should be subject to contextual control. This prediction was tested in Experiment 1, where automatic imitation was measured in red and blue contexts, both before and after two sessions of countermirror training completed in either red or blue contexts. The purpose of Experiment 2 was to confirm that any context specificity observed in Experiment 1 was due, as the ASL model suggests, to conflict between preexperimental learning and countermirror training and not to an artifact of procedure.

Experiment 1

Our first experiment sought to test whether countermirror learning is context-specific. In the first of four sessions, two separate pretests were conducted to establish participants' baseline automatic imitation effects in distinctive red and blue contexts. During the second and third sessions, participants received countermirror training in either the red or the blue contexts. In the final session, two separate posttests were conducted to establish participants' residual automatic imitation effects in both the red and blue contexts. Context specificity was indexed by comparing the magnitude of the pre- to posttest reduction in automatic imitation when participants were tested in the context in which they received

countermirror training and in their untrained context. If the MNs responsible for automatic imitation acquire their properties through associative learning, countermirror learning should behave like counterconditioning—it should show context specificity due to the conflict between the first-learned mirror associations and the second-learned countermirror associations.

Method

Participants. Sixteen healthy adults (five men) with a mean age of 22.4 years served as participants in the experiment in return for a small honorarium. All were right-handed, had normal or corrected-to-normal vision, and were naive to the purpose of the experiment. Participants were assigned randomly to either the train-red or train-blue groups in equal numbers. The study was approved by the University College London ethics committee and was performed in accordance with the ethical standards set out in the 1964 Declaration of Helsinki.

Apparatus and stimuli. The stimuli used in Experiment 1 consisted of 12 digital images of a model's right hand in naturalistic tones (see Figure 1). Six of the images were presented against a red background, and six against a blue background. Each color set comprised images of male and female neutral hands, male and female closed hands, and male and female open hands. The open stimulus showed fingers and thumb splayed. The male stimulus subtended approximately 17° of visual angle horizontally and 20° vertically, whereas the female stimulus subtended approximately 16° of visual angle both horizontally and vertically. The closed stimulus depicted a fist. The male stimulus subtended approximately 11° horizontally and 14° vertically, and the female stimulus
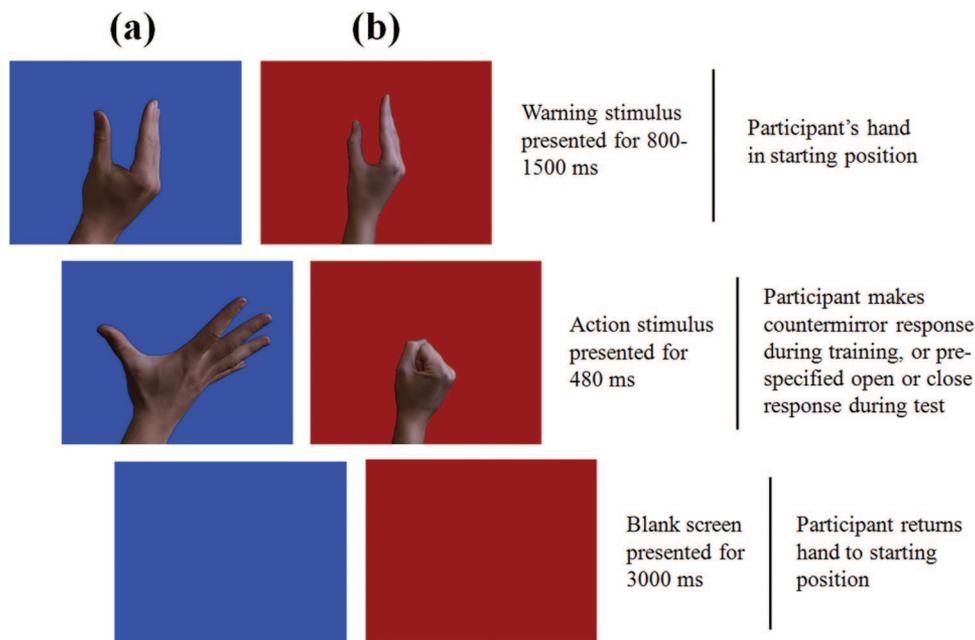
Figure 1. Display sequences for (a) male-hand open-stimulus trials in the blue context and (b) female-hand closed-stimulus trials in the red context. During training, participants made the countermirror response to the onset of the action stimulus (open responses to closed stimuli, closed responses to open stimuli). On test trials, participants made prespecified responses to the onset of the action stimulus; open-hand responses in one block and closed-hand responses in the other.

subtended approximately 8° horizontally and 12° vertically. In the neutral hand stimulus, fingers were shown together, pointing upward in parallel with the thumb. Both training and test trials were presented in color on a laptop PC with a 38-cm screen (resolution: 1,024 pixels × 678 pixels).

Contexts. Four elements were varied to provide two distinctive red and blue contexts. As described earlier, hand stimuli were presented against either red or blue backgrounds. In addition, the testing cubicle was lit by either red or blue light, provided by a Eurolite PAR-38 RGB LED spotlight. The experimental procedure required the use of an armrest to support the participants' hands and an occluder to prevent them from observing their own responses. Distinctive armrests and occluders were constructed for use in the red and blue contexts. The occluders were identical in all features except their color (either red or blue). The armrests were identical in size (15 cm × 35 cm × 25 cm) but differed in both color and surface texture. The red armrest was covered in a red coarse woolen fabric. The blue armrest was covered with a fine-grain plastic material. Display backgrounds (Cook et al., 2010; Nelson et al., 2011) and lighting changes (Van Gucht, Vansteenwegen, Beckers, & Van den Bergh, 2008; Vansteenwegen et al., 2005) have been shown to be effective context manipulations in single-room procedures.

Data recording and analysis. Both the training and test procedures took the form of reaction time (RT) tasks in which electromyography (EMG) was used to establish response onset. Recordings were taken from the first dorsal interosseus muscle using disposable surface electrodes manufactured by Unomedical Limited. The EMG signal was amplified, mains-hum filtered at 50 Hz, and digitized at 2.5 kHz. They were rectified and smoothed using a dual-pass Butterworth filter with cutoff frequencies of 20 Hz and 1,000 Hz. The EMG signal was registered for 100 ms before the onset of the imperative stimulus (see later) to define the baseline. A window of 20 ms was then shifted incrementally over the raw data in 1-ms steps. Response onset was defined as the start of the earliest 20-ms window following presentation of the imperative stimulus in which the standard deviation for that window, and for the following 20-ms interval, was greater than 2.75 times the standard deviation of the baseline. That this criterion reasonably defined response onset was verified by sight for every training and test trial.

Procedure. The experiment was conducted over four sessions, each completed approximately 24 hr apart. During the first session participants completed two test procedures to establish their baseline automatic imitation effects in the red and blue contexts. In Sessions 2 and 3, participants completed six blocks of countermirror training spread evenly over the 2 days, in either the red or blue context. In the final session, participants' residual automatic imitation effects were again measured in the red and blue contexts. The order in which participants completed the red and blue tests was counterbalanced but was held constant across Sessions 1 and 4.

In all four sessions, participants sat at a viewing distance of approximately 60 cm with their shoulders parallel to the stimulus display. Participants' arms were bent at the elbow, with their forearm positioned to face downward, also parallel to the display. The elbow and forearm were supported by an armrest, with both the hand and forearm occluded from view. Each participant's hand and wrist were positioned such that their fingers moved upward

during open responses and downward during close responses. Stimulus postures were presented in the lateral plane (left–right), thus ensuring that response movements were orthogonal to stimulus postures throughout. This feature of the design allows automatic imitation to be isolated from left–right spatial compatibility.

The test procedure was a simple RT task (see Figure 1), in which EMG recording was used to establish response onset. Tests comprised two blocks of 80 trials during which participants made speeded prespecified movements (hand-open responses in one block, hand-close responses in the other) in response to the onset of open and closed stimuli. This factorial manipulation constitutes a stimulus–response compatibility (SRC) design whereby responses can be either compatible with the observed stimulus (e.g., hand-open response to hand-open stimulus) or incompatible (e.g., hand-open response to hand-close stimulus). Each test trial started with the participant's hand in the neutral starting position and with a neutral hand warning stimulus on the screen. Thereafter participants were required to make the prespecified response as soon as an action stimulus appeared before returning to the neutral position ready for the next trial. The action stimulus was present for 480 ms until replaced by a blank display for 3,000 ms, prior to the warning stimulus for the next trial. Stimulus onset asynchrony (SOA) was varied randomly between 800 ms and 1,500 ms in 50-ms increments. The order in which participants completed the open and close blocks was counterbalanced across groups.

Twenty catch trials were included in each test block, in which the warning stimulus was displayed throughout the trial to which the participants had been instructed to make no response whatsoever. Because participants were making speeded prespecified responses, catch trials were included to prevent habitual, anticipatory responding and to encourage participants to continue to monitor what the stimulus was doing and to remain engaged with the task. On catch trials, the warning stimulus was presented for 1,980 ms before the 3,000-ms intertrial interval.

The training procedure took the form of a choice RT task (see Figure 1). Each trial required the participant to make either an open response to a closed-hand stimulus or a close response to an open-hand stimulus. Having made each response, participants returned to the starting position, ready for the next trial. The order of the action stimuli presentation was randomized during the training trials. The beginning of each trial was indicated by the appearance of the warning stimulus, which was then replaced by one of the action stimuli, presented for 480 ms. SOA was varied randomly between 800 ms and 1,500 ms in 50-ms increments. The hand depicted in the warning stimulus was identical to that in the subsequent action stimulus, giving rise to apparent motion. Following the offset of the action stimulus, the screen went blank for 3,000 ms, until the warning stimulus for the subsequent trial was presented. Each training block comprised 144 countermirror training trials. Half of the participants completed the countermirror training task in the red context, and the other half in the blue context.

Results and Discussion

Training and test trials in which participants made incorrect responses or no response, or where the point of movement onset was equivocal, were excluded from all further analyses (2.8% of training trials and 4.1% of test trials). Thereafter, any remaining

data points beyond 2.5 standard deviations of a participant's mean response latency for a given block were also excluded (2.0% of training trials and 2.9% of test trials). EMG signals on catch trials were examined to ensure that the participants obeyed task instructions but were excluded from all further analyses. During the test sessions, participants initiated movements on only 5.4% of catch trials, indicating that they were not making anticipatory responses on the stimulus trials.

Training. Figure 2 shows mean RTs for the groups trained in red and blue contexts. These training data were analyzed using a mixed-model analysis of variance (ANOVA) with training block (B1–B6) as a within-subject factor and training group (train-red, train-blue) as a between-subjects factor. Trend analysis revealed a highly significant linear decline across the six training blocks, $F(1, 14) = 19.83; p < .001; \eta^2 = .59$, suggestive of learning. This trend did not vary as a function of group, $F(1, 14) = 0.02; p > .80; \eta^2 = .00$, indicating that the improvement in training task performance was comparable. Although Figure 2 suggests that responses were faster in the red context than in the blue, no main effect of group was present, $F(1, 14) = 2.33; p > .14; \eta^2 = .14$, implying that overall RTs during the training task were broadly equivalent. Simple effects analysis revealed that the difference between the groups at Day 1, Block 1, was not significant, $t(14) = 0.87; p > .40$, indicating no difference in baseline performance. No higher order trends or other Trend × Group interactions were observed ($p > .07$).

Tests. Figure 3a shows the mean RTs observed at pre- and posttest, in the trained and untrained contexts, on compatible and incompatible trials. Figure 3b depicts the mean automatic imitation effects observed on the four tests (pretest in the trained context, pretest in the untrained context, posttest in the trained context, posttest in the untrained context). Automatic imitation reflects the tendency to execute imitative responses faster than nonimitative responses. The magnitude of the automatic imitation effect was therefore calculated by subtracting the mean RT on imitative trials

(open responses to open stimuli, closed responses to closed stimuli) from the mean RT on nonimitative trials (open responses to closed stimuli, closed responses to open stimuli) for each participant. The greater this RT difference, the stronger the tendency to imitate. In Table 1, performance is further broken down for the groups trained in the red and blue contexts.

The RT data were analyzed using a mixed-model ANOVA with test (pretest, posttest), context (trained, untrained), and SRC (compatible, incompatible) as within-subject factors and group (train-red, train-blue) as a between-subjects factor. The analysis revealed a highly significant main effect of SRC, $F(1, 14) = 98.23; p < .001; \eta^2 = .88$, whereby participants were slower to make incompatible responses ($M = 303.4$ ms; $SD = 71.6$ ms) than compatible responses ($M = 282.2$ ms; $SD = 68.9$ ms) indicative of automatic imitation. In addition, a marginally significant Test × Compatibility interaction was observed, $F(1, 14) = 3.94; p = .067; \eta^2 = .22$, indicating that automatic imitation effects were generally smaller at posttest ($M = 16.3$ ms; $SD = 15.1$ ms) than at pretest ($M = 26.2$ ms; $SD = 16.4$ ms). Crucially, this Test × Compatibility interaction varied as a function of context, $F(1, 14) = 7.46; p < .025; \eta^2 = .35$. Simple effects analysis indicated that there was a significant reduction in automatic imitation between the pretest ($M = 26.9$ ms; $SD = 14.5$ ms) and posttest ($M = 12.6$ ms; $SD = 15.3$ ms) when tested in the trained context, $t(15) = 2.89; p < .025$. In contrast, the reduction in automatic imitation between the pretest ($M = 25.5$ ms; $SD = 18.6$ ms) and posttest ($M = 20.1$ ms; $SD = 14.5$ ms) when tested in the untrained context was not significant, $t(15) = 1.05; p > .30$. This Test × Context × Compatibility interaction did not vary as a function of group, $F(1, 14) = 0.40; p > .5; \eta^2 = .03$.

In addition to the effects of principal interest just described, a significant Group × Compatibility interaction was observed, $F(1, 14) = 10.25; p < .025; \eta^2 = .42$. Those participants given countermirror training in the red context generally showed greater automatic imitation ($M = 28.1$ ms; $SD = 14.5$ ms) than those
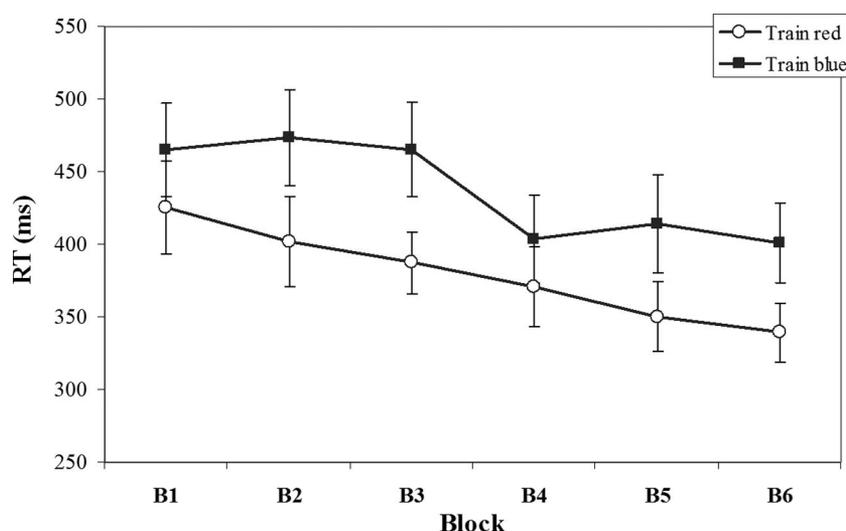

Figure 2. Mean RTs observed during training in Experiment 1, plotted across the six training blocks. Open circles represent the performance of the group trained in the red context, and filled squares represent the group trained in the blue context. Error bars represent the standard error of the mean. RT = reaction time; B = block.
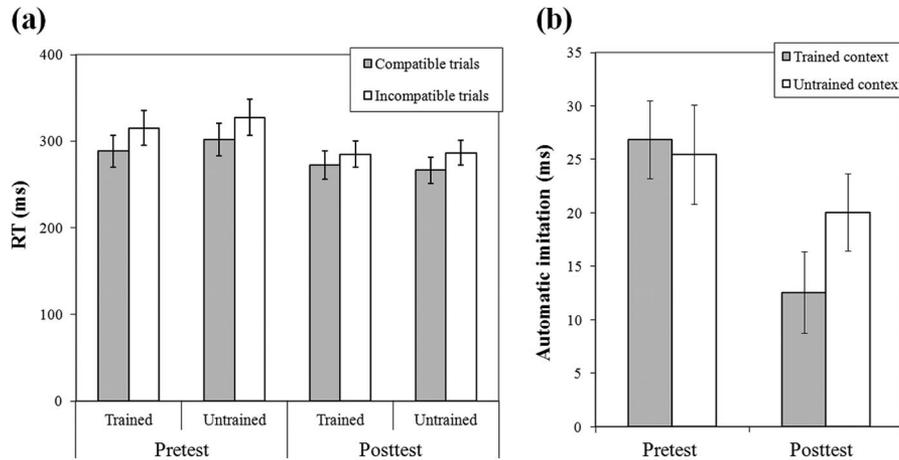
Figure 3.   (a) Mean RTs observed at pretest and posttest, in the trained and untrained contexts, on compatible and incompatible trials, and (b) automatic imitation effects observed at pretest and posttest in the trained and untrained contexts, calculated by subtracting mean RTs on compatible trials from mean RTs on incompatible trials. Error bars represent the standard error of the mean. RT = reaction time.

trained in the blue context ($M = 14.4$ ms; $SD = 15.5$ ms). A marginally significant main effect of test was also observed, $F(1, 14) = 3.94$; $p = .067$; $\eta^2 = .22$, indicating that participants generally responded faster at posttest ($M = 277.5$ ms; $SD = 60.5$ ms) than at pretest ($M = 308.2$ ms; $SD = 77.3$ ms). None of the other main effects or interactions approached significance ($p > .10$).

The results of Experiment 1 indicate that greater reductions in automatic imitation were seen when participants were tested in their trained context than in their untrained context. This finding suggests that countermirror learning behaves like countercondi-tioning, in that both show context specificity (Bouton & Peck, 1992). Associative accounts argue that counterconditioning comes under contextual control in order to resolve ambiguity (Bouton, 1993, 1994; Nelson, 2002). Rather than simply overwriting the original learning, there is considerable evidence that subsequent conditioning to the same stimulus sets up parallel, second-learned associations (Bouton & Peck, 1992; Brooks, Hale, Nelson, & Bouton, 1995). However, the conflict between the first- and second-learned associations renders the stimulus ambiguous: It is not clear what the appropriate behavior is in the presence of the stimulus. To resolve this ambiguity, the excitability of both sets of associations is modulated by the context. Second-learned associ-ations become active only in the trained context, whereas first-

learned associations are inhibited by the cues present in the trained context but remain active in all other contexts.

Experiment 2

The ASL model (Heyes, 2001, 2010a, 2010b; Ray & Heyes, 2011) proposes that automatic imitation, and the congruent MNs that are thought to mediate automatic imitation, are a product of sensorimotor associations acquired during development (e.g., through self-observation, synchronous activity, and while being imitated). This model therefore implies that the context specificity observed in Experiment 1 was due to conflict between the second-learned countermirror associations established by experimental training and the first-learned mirror associations acquired long before the experiment began.

Experiment 2 sought to confirm this interpretation by testing whether first-learned sensorimotor associations would generalize across contexts within our procedure. Novel stimulus–response (S-R) learning should generalize well to untrained contexts be-cause there is no conflict with preexperimental learning, and consequently the stimuli remain unambiguous. Evidence of context-specific learning in Experiment 2 would therefore indicate that the context specificity observed in Experiment 1 was not due

Table 1

Mean (SD) Reaction Times Observed During Experiment 1 in the Four Tests Shown for Participants Trained in the Red and Blue Contexts

	Red group		Blue group	
Variable	Compatible	Incompatible	Compatible	Incompatible
Pretest red	278.5 (96.7)	312.7 (106.5)	315.6 (41.6)	334.1 (55.3)
Pretest blue	288.2 (100.6)	320.7 (106.7)	298.0 (48.2)	317.5 (51.7)
Posttest red	256.3 (66.5)	276.6 (66.5)	277.9 (51.5)	292.6 (54.0)
Posttest blue	254.9 (62.6)	280.3 (62.6)	288.2 (62.5)	293.0 (57.8)

to conflict with preexperimental learning and may instead reflect an artifact of procedure.

We used a four-session design, identical to that employed in Experiment 1, to train arbitrary S-R mappings with abstract geometric shapes. Participants again made open- and closed-hand responses but this time to the onsets of geometric trapezoid forms. In the first session, they completed simple RT pretest procedures in the red and blue contexts to confirm the absence of any preexisting compatibility effects. They then completed two training sessions with a choice RT task, either in the red or blue contexts, where they learned to make open and closed responses to the onset of top- and bottom-heavy trapezoids, respectively. In the final session they were tested again in both the red and blue contexts to determine the magnitude of their newly acquired SRC effect.

Method

Participants. A further 16 healthy adults (4 men) with a mean age of 21.9 years served as participants in the experiment in return for a small honorarium. All were right-handed, had normal or corrected-to-normal vision, and were naive to the purpose of the experiment. Participants were randomly assigned to either the train-red or train-blue training group in equal numbers.

Apparatus and stimuli. The stimuli used in Experiment 2 consisted of 12 digital images of gray quadrilaterals (see Figure 4). Two sets of lighter and darker stimuli, each with different aspect ratios were employed to parallel the pigmentation and scale variation in the male and female hand stimuli. Six of the images were presented against a red background, and six against a blue background. Each color set included two rectangles, one lighter and one darker, and four isosceles trapezoids bisected by a horizontal black line, one top-heavy in a lighter tone, one top-heavy in a darker tone, one bottom-heavy in a lighter tone, and one bottom-heavy in a darker tone. The lighter gray rectangle (160 on a 0–255 scale) had an aspect ratio of 1:1.23 and subtended approximately 12° horizontally. The darker rectangle (140 on a 0–255 scale) had an aspect ratio of 1:1.57 and subtended approximately 9° horizontally. The lighter gray trapezoids subtended 14° at the wider end (170 on a 0–255 scale) and 10° at the narrower end (150 on a 0–255 scale). The darker gray trapezoids subtended 11° at the wider end (150 on a 0–255 scale) and 7° at the narrower end (130 on a 0–255 scale).

Procedure and design. As in Experiment 1, the order in which participants completed the red and blue tests was counterbalanced but was held constant across pre- and posttest. The test procedure employed in both contexts again took the form of a simple RT task. Participants made speeded prespecified movements (open responses in one block, closed in the other) in response to the onset of top-heavy and bottom-heavy trapezoid stimuli (see Figure 4). Each test trial started with the participant's hand in the neutral starting position and with a rectangular warning stimulus on the screen. Thereafter participants were required to make the prespecified response as soon as a trapezoid stimulus appeared and then return to the neutral position ready for the next trial. The rectangle-trapezoid display sequence gave rise to apparent motion of either the top or bottom of the rectangle moving forward, depending on the trapezoid presented. The trapezoid stimulus was presented for 480 ms until replaced by a blank display for 3,000 ms, prior to the warning stimulus for the next trial. SOA was varied randomly between 800 ms and 1,500 ms in 50-ms increments. Twenty catch trials were included in each test
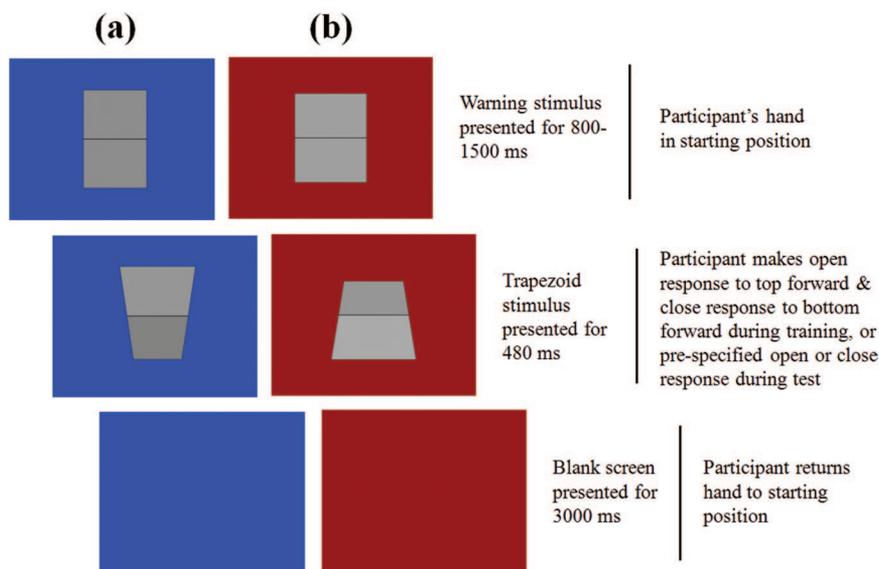
Figure 4. Display sequences for (a) larger aspect ratio top-heavy sequence in the blue context and (b) smaller aspect ratio bottom-heavy sequence in the red context. In each case, the presentation of a top- or bottom-heavy trapezoid gave the appearance of the rectangle falling either toward or away from the participant. During training, participants made open-hand responses when the top appeared to move forward and closed-hand responses when the bottom appeared to move forward. On test trials, participants made prespecified responses to the onset of the trapezoid stimulus: open-hand responses in one block, closed-hand in the other.

block. On catch trials, the warning stimulus was presented for 1,980 ms before the 3,000-ms intertrial interval. The order in which participants completed the open and closed blocks was counterbalanced across groups. The test procedure was therefore identical to that employed in Experiment 1.

The training procedure again took the form of a choice RT task (see Figure 4). Each trial required the participant to make either an open response to a top-forward stimulus or a closed response to a bottom-forward stimulus. To ensure that the design and analyses were comparable with those of Experiment 1, this arbitrary S-R mapping was not counterbalanced. The order of stimulus presentation during the training trials was randomized. The beginning of each trial was indicated by the appearance of the rectangle warning stimulus, which was then replaced by one of the trapezoid stimuli, presented for 480 ms. SOA was varied randomly between 800 ms and 1,500 ms in 50-ms increments. Following the offset of the trapezoid stimulus, the screen went blank for 3,000 ms, until the warning stimulus for the subsequent trial was presented. Each training block comprised 144 training trials. Half of the participants completed the training task in the red context, and half in the blue context.

Results and Discussion

Training and test trials in which participants made incorrect responses or no response, or where the point of movement onset was equivocal, were excluded from all further analyses (3.4% of training trials and 4.5% of test trials). Thereafter, any remaining data points beyond 2.5 standard deviations of a participant's mean response latency for a given block were also excluded (3.0% of training trials and 3.3% of test trials). EMG signals on catch trials were examined to ensure that participants obeyed task instructions but were excluded from all further analyses. During the test sessions, participants initiated movements on only 5.7% of catch trials, indicating that they were not making anticipatory responses on the stimulus trials.

Training. Figure 5 shows mean RTs for the groups trained in red and blue contexts. A mixed-model ANOVA with training block (B1–B6) as a within-subject factor and training group (train-
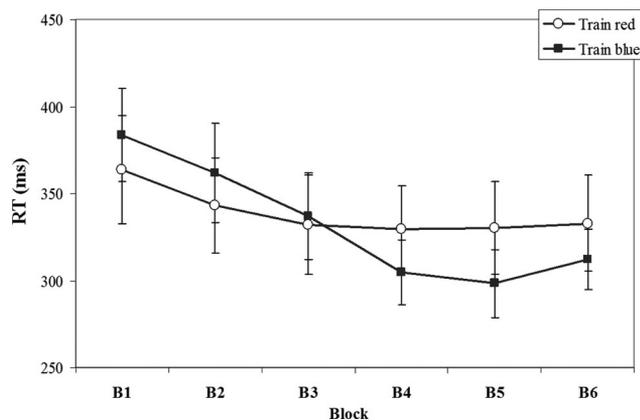
red, train-blue) as a between-subjects factor revealed a highly significant linear decline across the six training blocks, $F(1, 14) = 14.19$; $p < .01$; $\eta^2 = .50$, suggestive of learning. The Group $\times$ Linear Trend interaction failed to reach significance, $F(1, 14) = 3.47$; $p > .08$; $\eta^2 = .19$, indicating that the linear decline was broadly comparable across groups. Trend analysis also revealed a significant quadratic trend, $F(1, 14) = 14.07$; $p < .01$; $\eta^2 = .50$; however, this did not vary as a function of group, $F(1, 14) = 0.66$; $p > .40$; $\eta^2 = .05$. No main effect of group was present, $F(1, 14) = 0.03$; $p > .80$; $\eta^2 = .00$, implying that overall RTs during the training task were also broadly equivalent. Simple effects analysis revealed that the difference between the groups at Day 1, Block 1, was not significant, $t(14) = 0.49$; $p > .60$, indicating that baseline performance was comparable.

Tests. Figure 6 shows the mean RTs observed at pre- and posttest, in the trained and untrained contexts, on compatible and incompatible trials. Figure 6 also depicts the mean compatibility effects seen on the four tests (pretest in the trained context, pretest in the untrained context, posttest in the trained context, posttest in the untrained context). Because the trained S-R mappings were open to top-forward and closed to bottom-forward, the size of each SRC effect was calculated by subtracting the mean RT on compatible trials (open to top-forward, closed to bottom-forward) from the mean RT on incompatible trials (open to bottom-forward, closed to top-forward). The greater the RT difference, the stronger the participants' tendency to execute the trained response in the presence of the test stimuli. These SRC effects are conceptually equivalent to the automatic imitation effects calculated in Experiment 1. Performance is further broken down for the groups trained in the red and blue contexts in Table 2.

The RT data were analyzed using a mixed-model ANOVA with test (pretest, posttest), context (trained, untrained), and SRC (compatible, incompatible) as within-subject factors and group (train-red, train-blue) as a between-subjects factor. The analysis revealed a significant main effect of SRC, $F(1, 14) = 12.60$; $p < .01$; $\eta^2 = .47$, whereby participants were faster to make responses compatible with the trained mapping ($M = 280.8$ ms; $SD = 52.3$ ms) than incompatible responses ($M = 284.1$ ms; $SD = 51.9$ ms) when collapsed across test. In addition, a significant Test $\times$ Compatibility interaction was observed, $F(1, 14) = 9.37$; $p < .01$; $\eta^2 = .40$, indicating that SRC effects were larger at posttest ($M = 7.08$ ms; $SD = 6.62$ ms) than at pretest ($M = -0.61$ ms; $SD = 5.43$ ms). Crucially, this Test $\times$ Compatibility interaction did not vary as a function of context, $F(1, 14) = 0.27$; $p > .60$; $\eta^2 = .02$, indicating that the change in SRC was equivalent in trained and untrained contexts. Moreover, the Test $\times$ Compatibility $\times$ Context interaction was comparable in both groups, $F(1, 14) = 0.18$; $p > .65$; $\eta^2 = .01$. No other main effects or interactions approached significance ($p > .25$).

In Experiment 1, countermirror learning was context-specific; the associations acquired manifested more strongly in the trained than in the untrained context. In contrast, the results from Experiment 2 show that novel S-R learning generalizes to untrained contexts. Given that identical designs were used in the two experiments, this contrast indicates that the context specificity observed in Experiment 1 was not an artifact of procedure. Rather, the results of Experiment 2 accord with the claim that, in Experiment 1, context specificity was generated by a conflict between second-

Figure 5. Mean RTs observed during training in Experiment 2, plotted across the six training blocks. Open circles represent the performance of the group trained in the red context, and filled squares represent the group trained in the blue context. Error bars represent the standard error of the mean. RT = reaction time; B = block.
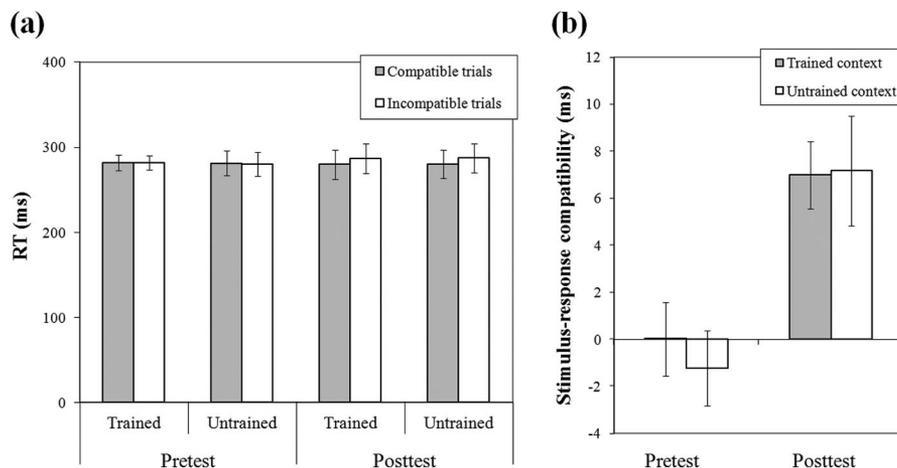
Figure 6. (a) Mean RTs observed at pretest and posttest, in the trained and untrained contexts, on compatible and incompatible trials, and (b) stimulus–response compatibility effects observed at pretest and posttest in the trained and untrained contexts, calculated by subtracting mean RTs on compatible trials from mean RTs on incompatible trials. Error bars represent the standard error of the mean. RT = reaction time.

learned countermirror associations and first-learned associations established during ontogeny.

General Discussion

The present study tested the hypothesis, advanced by the ASL model, that when the sight of an action is associated with rival mirror and countermirror responses, this ambiguity is resolved through contextual modulation—the same process thought to resolve ambiguity resulting from conflicting associations in counterconditioning experiments (Bouton, 1993, 1994; Nelson, 2002). The results were affirmative. When open and closed hand stimuli were rendered ambiguous through periods of countermirror training, the second-learned countermirror associations manifested more strongly in the trained context, resulting in less automatic imitation. Our second experiment confirmed that this context specificity was due to conflict between second-learned countermirror associations and first-learned mirror associations established during the course of normal, preexperimental development by demonstrating that analogous first-learned arbitrary sensorimotor associations do generalize across our context manipulation.

Contextual Modulation of Automatic Imitation

Several previous findings have indicated that automatic imitation may be modified through sensorimotor training (Cook et al.,

2010; Gillmeister et al., 2008; Heyes et al., 2005; Press, Gillmeister, & Heyes, 2007). Crucially, however, the present data provide further evidence that this learning is associative—that it is mediated by the same processes responsible for Pavlovian and instrumental conditioning in humans and animals. Counterconditioning and renewal effects demonstrate that second-learned associations show greater context specificity than do the first associations formed with a novel stimulus (Bouton, 1994; Bouton & King, 1983; Nelson, 2002; Nelson et al., 2011; Peck & Bouton, 1990). That the sensorimotor associations established during countermirror learning are modulated by context argues that countermirror associations are equivalent to second-learned associations acquired during counterconditioning. This finding suggests a clear parallel between mirror associations acquired during development and first-learned associations established during conditioning. In this respect the present data accord with evidence that countermirror learning is sensitive to the contingency between the sensory and motor representations—the extent to which action observation predicts the incompatible response (Cook et al., 2010). Insofar as contextual modulation and contingency sensitivity are both predictions derived from conditioning experiments, these effects support the view that the acquisition of conceptually equivalent mirror and countermirror sensorimotor links is mediated by phylogenetically ancient mechanisms of associative learning (Heyes, 2001, 2010a, 2010b; Ray & Heyes, 2011).

Table 2

Mean (SD) Reaction Times Observed During Experiment 2 in the Four Tests Shown for Participants Trained in the Red and Blue Contexts

	Red group		Blue group	
Variable	Compatible	Incompatible	Compatible	Incompatible
Pretest red	286.2 (38.9)	284.9 (37.3)	265.4 (40.7)	264.9 (41.0)
Pretest blue	297.3 (69.9)	295.3 (69.8)	277.4 (36.2)	278.8 (32.4)
Posttest red	297.1 (56.2)	302.9 (58.4)	258.2 (59.3)	264.9 (60.6)
Posttest blue	302.3 (72.6)	310.0 (74.1)	262.8 (78.5)	271.0 (78.3)

It might be suggested that countermirror training reduces automatic imitation, not by establishing new sensorimotor associations but by encouraging participants to use an intentional, "do opposite" response strategy (Heyes, 2011). The context specificity observed in Experiment 1 suggests that this is not the case. One of the defining characteristics of intentional response strategies is their flexibility. For example, that incompatible stimulus–response training transfers from one spatial task to another has been cited as evidence that learning is strategic (Vu, 2007). In contrast, the context specificity of countermirror learning shows that it is relatively inflexible.

Associative accounts argue that the context specificity of second-learned associations emerges as a means to resolve ambiguity (Bouton, 1993, 1994; Nelson, 2002). Rather than overwrite or unlearn existing associations, there is considerable evidence that extinction and counterconditioning establish additional parallel associations (Bouton & Peck, 1992; Brooks et al., 1995). However, being associated with two opposing responses renders the stimulus ambiguous. Because of the conflict between the first- and second-learned associations, it is not clear what the appropriate behavior is in the presence of the stimulus. To resolve this ambiguity, the excitability of the first- and second-learned associations may be modulated by the context. Specifically, counterconditioning may create associations that inhibit the original response as well as excite the second-learned response, both of which may be selectively activated by the counterconditioning context. When applied to the present paradigm this account argues that countermirror training sets up second-learned associations that inhibit the mirror response and excite the appropriate countermirror response. Both inhibitory and excitatory countermirror associations are selectively "turned on" by the contextual cues present in the training environment. When participants leave the training context, the newly acquired associations become less excitable.

The contrasting behavior of first- and second-learned associations suggests that the temporal order in which one encounters sensorimotor contingencies is an important factor in determining which responses generalize to novel contexts. In particular, the nature of early sensorimotor experience may be crucial. Our results suggest that whichever associations are acquired first, be they mirror or countermirror, will generalize readily across contexts, whereas associations acquired subsequently will show greater context specificity. Parents and caregivers imitate newborns (Malatesta & Haviland, 1982; Pawlby, 1977), and these interactions are likely to provide some of the earliest experience of contingencies between action execution (e.g., neonate executes smile) and action observation (e.g., neonate observes caregiver smiling; Ray & Heyes, 2011). The early acquisition of mirror associations may cause "mirroring" to become the default, context-general response that manifests in novel situations. If, however, newborns were first exposed to predominantly nonmatching sensorimotor contingencies, automatic countermirror or complementary responses might become prepotent in novel contexts.

In the present study, context was manipulated by changing visual (lighting, background colors) and tactile (texture of the armrest) variables. However, in addition to physical variables, context may also encompass internal states. If extinction of a conditioned response is conducted while participants are receiving tranquilizers (Bouton, Kenney, & Rosengard, 1990) or alcohol (Cunningham, 1979), learning is found to be state-dependent. A

renewal effect is observed whereby the conditioned response is renewed when the effects of the drug manipulations wear off. Several nonmatching sensorimotor contingencies may also be modulated by the context provided by internal state. For example, sports provide a wealth of nonmatching contingencies. In tennis, the execution of a serve is predictive of the sight of a return, and in boxing the execution of a jab predicts the sight of an opponent raising his guard. However, while sportsmen and -women experience these contingencies, levels of cortisol and adrenalin, heartrate, and body temperature are frequently elevated. These internal contexts may serve to modulate conflicting responses, by changing the relative excitability of mirror and countermirror associations in different situations.

Insofar as the present study did not include neurophysiological methods, we cannot specify precisely where in the brain these learning effects occurred. One possibility is that the learning observed reflects the acquisition of arbitrary stimulus–response associations thought to be represented within the dorsal premotor cortex (Passingham, 1993; Wise & Murray, 2000). However, this account is not compelling, because it implies that the action stimuli were perceived not as actions but as arbitrary visual stimuli. The robust automatic imitation effects seen at pretest indicate that the action stimuli were sufficiently lifelike to excite previously learned sensorimotor associations. Rather than reflecting associations acquired with arbitrary stimuli, these data demonstrate that sensory representations of actions came to excite noncongruent motor representations, as a result of countermirror training. Based on a purely functional definition, these countermirror training effects are therefore likely to be mediated by MNs (i.e., units that respond to both the sight and execution of an action). Any alternative account would appear to require the existence of a new class of motor neuron, one that also responds to action observation but is somehow qualitatively distinct from MNs.

Implications for the Functioning of the Mirror Neuron System

Assuming (a) that automatic imitation is a behavioral product of congruent MNs and (b) that countermirror learning occurs within the MNS, our findings may have important implications for the functioning of this system. In the present study, the open and closed hand stimuli were rendered ambiguous by periods of countermirror training. However, there is evidence that sensorimotor ambiguity may be a typical feature of the MNS and not merely a product of laboratory S-R training. Substantial proportions of macaque MNs (di Pellegrino et al., 1992; Ferrari et al., 2003; Gallese et al., 1996; Rozzi et al., 2008; Umiltà et al., 2001) and human sensorimotor units (Mukamel et al., 2010) discharge indiscriminately during the observation of multiple actions or selectively during the observation and execution of different actions. The resulting sensorimotor ambiguity is challenging for theories that posit that MNs make a functional contribution to action understanding (Rizzolatti & Craighero, 2004; Rizzolatti et al., 1996), imitation (Heyes, 2011; Iacoboni, 2009), or generic action selection (Hickok & Hauser, 2010). Because the sight of an action excites multiple motor representations, it is unclear which action the observer should "understand" or "select." However, modulation of MN responses by context might help to explain how the MNS can contribute to coherent behavior in spite of the conflicting responses of single MNs; for

example, how observation of the same action might trigger an imitative response in one context but a complementary or countermirror response in another.

Much of the contingent sensorimotor experience we receive in everyday life involves matching; the execution of an action predicts the observation of the same action. However, we are also exposed to nonmatching sensorimotor contingencies, where the execution of one action predicts the observation a different action. During coordinated instrumental action, the sight of another agent releasing an object reliably predicts the performance of a grasping action (Newman-Norlund, van Schie, van Zuijlen, & Bekkering, 2007; van Schie, van Waterschoot, & Bekkering, 2008). Similarly, in social control situations, involving dominance and submission, expansive gestures by one interactant predict contraction movements by the other, and vice versa (Tiedens & Fragale, 2003). The contexts in which fMRI and single-cell recording takes place are necessarily different from the contexts in which one receives nonmatching experience. However, where nonmatching contingencies represent second-learned associations, neural populations coding such relationships may be evident only in the presence of specific contextual cues. Taking steps to invoke learning contexts during neuroimaging and single-cell procedures may therefore reveal greater numbers of noncongruent MNs.

Contextual modulation may also help explain why MNs appear to code abstract "motor goals." MNs respond differently to the sight of an experimenter grasping a food item depending on whether the goal of the action is to eat the food or to place it in a shoulder-mounted cup (Bonini et al., 2010; Fogassi et al., 2005). That MN responses differed before the observed action trajectories could be differentiated is taken as evidence that MNs help one understand the motor intentions of others. However, the present data demonstrate that a simple associative account can be advanced to explain these data, without postulating any role of MNs in higher order action understanding. Prior to the experiment, it is reasonable to assume that the macaques had ample opportunity to acquire S-R associations between the sight of grasping and grasp-to-eat motor programs. During the experiment, the animals acquired further S-R associations such that the sight of grasping could also excite grasp-to-place motor programs. Because these second-learned associations served to render the sight of grasping ambiguous, they became subject to contextual control. Crucially, whenever the monkeys were required to grasp-to-place, the target cup was always present, either in front of the macaques or on their shoulder. The second-learned grasp-to-place associations were likely to have been modulated by the presence of this salient contextual cue. When the macaques subsequently observed grasping, in either the presence or absence of the cup, MNs were either excited or inhibited by this context, thus giving the impression that they were coding action intention.

In summary, while countermirror learning shows context specificity, the acquisition of arbitrary S-R associations generalizes well to untrained contexts. Associative accounts argue that countermirror learning comes under contextual control because it establishes second-learned associations that render the sight of actions ambiguous. In contrast, novel S-R associations generalize to untrained contexts because there is no conflict with previous learning. That the sensorimotor associations established during countermirror learning are modulated by context indicates that countermirror associations are equivalent to second-learned asso-

ciations acquired during counterconditioning experiments. Our results therefore suggest a parallel between mirror associations acquired during development and first-learned excitatory associations established during conditioning. We have argued that contextual modulation emerges to resolve the conflict caused by countermirror training—a laboratory treatment that participants are unlikely to encounter in their daily lives. However, neurophysiological studies have indicated that ambiguity may be a typical feature of both the human and macaque MNS. The findings presented here suggest that contextual modulation may play a key role in ensuring that the MNS contributes to coherent patterns of behavior in spite of the conflicting responses of individual MNs.

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