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Mirror and (absence of) counter-mirror responses to action sounds measured with TMS

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Abstract

To what extent is the mirror neuron mechanism malleable to experience? The answer to this question can help characterising its ontogeny and its role in social cognition. Some suggest that it develops through sensorimotor associations congruent with our own actions. Others argue for its extreme volatility that will encode any sensorimotor association in the environment. Here, we added to this debate by exploring the effects of short goal-directed ‘mirror’ and ‘counter-mirror’ trainings (a ‘mirror’ training is defined as the first type of training encountered by the participants) on human auditory mirror motor-evoked potentials (MEPs). We recorded MEPs in response to two tones void of previous motor meaning, before and after mirror and counter-mirror trainings in which participants generated two tones of different pitch by performing free-choice button presses. The results showed that mirror MEPs, once established, were protected against an equivalent counter-mirror experience: they became manifest very rapidly and the same number of training trials that lead to the initial association did not suffice to reverse the MEP pattern. This steadiness of the association argues that, by serving direct-matching purposes, the mirror mechanism is a good solution for social cognition.

Key words: motor; action sounds; mirror neurons; transcranial magnetic stimulation; motor and sensory learning

Introduction

Over the last years, transcranial magnetic stimulation (TMS) and neuroimaging studies (reviewed in Aglioti and Pazzaglia, 2011) have revealed a fundamental functional equivalence between action execution and action perception (originally proposed by James, 1890), for which hearing the sounds of an action executed by another individual automatically awakens a corresponding motor representation in the brain of the listener (Ticini et al., 2012). A rare intracranial EEG recording in an epileptic 12-year-old girl provided a direct demonstration of this phenomenon: the sound of finger-clicks activated her hand’s motor area as if she was performing finger-clicks herself

(Lepage et al., 2010a). These responses are analogous to those identified a decade ago in non-human primates where neurophysiological studies found a class of cells in the motor cortex (known as ‘mirror neurons’; reviewed in Rizzolatti and Craighero, 2004) which activity was triggered when the monkey executed a motor act as well as when it observed or heard the sound of the same action executed by another individual (Keyzers et al., 2003; Kohler et al., 2002). In humans, the existence of a ‘mirror neuron mechanism’ (Fadiga et al., 1995; Nishitani and Hari, 2000; Oberman et al., 2007; Borroni et al., 2008; Etzel et al., 2008; Keyzers and Gazzola, 2009; Kilner et al., 2009; Mukamel et al., 2010; Oosterhof et al., 2010, 2012) was further

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substantiated by brain damage (Pazzaglia et al., 2008) and inactivation (D'Ausilio et al., 2009; Möttönen and Watkins, 2009) studies.

Characterising the ontogeny of the mirror neuron mechanism has been a challenge of recent experimental and theoretical work as its role may extend from social cognition (Gallese, 2007), to action understanding (Rizzolatti and Craighero, 2004) and to language development (Rizzolatti and Arbib, 1998; Theoret and Pascual-Leone, 2002; Arbib, 2005). Two main ideas have prevailed.

On the one hand, the associative account of mirror neuron origins emphasises the role of experience and suggests that the mirror properties of the brain may develop through simple stimulus–response (or sensory–motor) associations that link an action to any stimulus (Heyes, 2010). On the other, it has been proposed that Hebbian plasticity in synapses—connecting the re-afferent sensory representation of the consequences of our actions with the motor programs that caused these consequences (hence, motor–sensory)—may be the neural mechanism that leads to the emergence of mirror neurons (Keysers and Perrett, 2004; Keysers and Gazzola, 2014). This Hebbian hypothesis finds support in the fact that a few hours of piano lessons, in which a participant experiences the causality between pressing keyboard keys and hearing the tones they produce, suffices to generate cortical responses overlapping with motor execution upon hearing a learned piano melody (Lahav et al., 2007; Novembre et al., 2012, 2014; D'Ausilio et al., 2006; Haueisen and Knösche, 2001).

An important debate in this line of research focuses on the volatility and arbitrariness of such associations. Some argue that we are endowed with a mechanism that channels the development towards sensorimotor associations congruent with our own actions (Del Giudice et al., 2009). Others have emphasised that this system is volatile, and will encode any sensorimotor association in the environment. The latter hypothesis is grounded on data showing that a short imitative training or ‘associative counter-mirror training’ (i.e. when participants are taught to respond to an observed behaviour with an similar or opposite motor act; see Cavallo et al., 2013; Catmur et al., 2007, 2008, 2011) can enhance (Press et al., 2007; Wiggett et al., 2012), abolish (Cook et al., 2010, 2012; Gillmeister et al., 2008; Heyes et al., 2005; Wiggett et al., 2011) or even reverse (e.g. Catmur et al., 2007) pre-existing mirror responses. In other words, to shed doubts on the fact that plasticity will generate neurons that associate the perception of a particular action with the motor program to perform this action, this line relies on the demonstration that sensory–motor associative experience changes the pattern of mirror responses. However, there is no consensus on this, yet (e.g. Cook et al., 2014; Rizzolatti, 2014; Keysers et al., 2014). For instance, a recent study indicated that counter-mirror associative trainings may have a limited influence on primarily congruent mirror responses (Barchiesi and Cattaneo, 2013; but see also Cavallo et al., 2013). Further investigation is required to understand plasticity within this class of associations.

Crucially, associative counter-mirror experiments generally employed non-transitive (devoid of a goal) motor acts and stimulus–response paradigms, in which the stimulus *precedes* the participants’ motor responses rather than *vice versa* (i.e. sensory–motor). However, based on what we know about the properties of Hebbian plasticity, other authors have argued that mirror properties must develop when voluntary actions are *causally and contingently* associated with their sensory effects (Rizzolatti et al., 1996; Keysers and Perrett, 2004; Casile et al., 2011; Keysers et al., 2014). That is, when goal-directed actions cause the re-afferent sensory stimulus rather than *vice versa* (i.e. motor–sensory). Once this correspondence between motor and

sensory brain centres is established, the incoming sensory information can flow in a forward direction, from visual or auditory stimuli to actions, triggering a mirror response in parietal and motor areas (Rizzolatti, 2014).

In our TMS experiment we set out to investigate whether mirror MEP responses to action-sounds, generated by causally associating goal-directed actions with arbitrary sounds, are susceptible to opposite but equivalent experience. We employed an established paradigm in which, in a series of goal-directed mirror and counter-mirror trainings, participants generated two arbitrary tones of different pitch by pressing two buttons with their right index and little finger, respectively (see Elsner and Hommel, 2001; Ticini et al., 2012; Figure 1A). Before and after each series of training, we measured the sound-related modulations in the listeners’ motor cortex during passive listening to the two tones by recording TMS-induced MEPs from the hand muscles involved: the abductor digiti minimi (ADM; little finger muscle) and first dorsal interosseous (FDI; index finger muscle). The amplitude of the MEPs recorded from selected muscles in response to a single magnetic TMS pulse applied over the primary motor cortex is a reliable and specific index of motor mirror responses, i.e. the activation of motor programs matching perceived actions (Fadiga et al., 1995). In an earlier work (Ticini et al., 2012), we used this method to measure newly established auditory mirror MEPs. In that occasion, we found that a very short goal-directed training was sufficient for the brain of the listeners to learn to respond to action-related sounds in a mirror-like fashion. This outcome supported the view that this type of mirror responses can quickly develop through goal-directed experience. In the present study, we aimed at replicating our previous result and at further testing our experimental question by introducing a series of goal-directed ‘counter-mirror’ trainings.

We expected to rapidly establish a higher-order correspondence between auditory and motor aspects of actions (see Ticini et al., 2012) when individuals causally associated their actions with an auditory effect (or action-goal; i.e. the act of generating a particular tone by pressing a specific button). Moreover, we predicted two possible scenarios. On the one hand, if this correspondence is permanently represented in the brain (see also Experiment 2 in Ticini et al., 2012), then newly developed mirror MEP responses should be protected against opposite equivalent (i.e. goal-directed counter-mirror) experience. On the other, if the goal-directed counter-mirror training is capable of reversing mirror responses, then we expected to replicate the results of previous associative work (e.g. Catmur et al., 2007; Catmur and Heyes, 2017) by recording an opposite pattern of MEP after the counter-mirror trainings. If that were the case, we wanted to test whether the plastic changes of the mirror mechanism could be replicated over time and with a different (reduced) number of trials. We designed the experiment accordingly, by organising the mirror and counter-mirror trainings in four Cycles of different lengths.

Materials and methods

Participants and experimental protocol

The experiment was carried out on sixteen (six females) right-handed healthy undergraduate students, with ethical-committee approval and informed written consent. We determined the required size through the G* power software (Faul et al., 2009) by setting the expected effect size at 0.28 (estimated from previous studies on mirror and counter-mirror effects; Ticini et al., 2012; Barchiesi and Cattaneo, 2013; Cavallo et al., 2013; Catmur et al., 2007), the significance level at 0.05, and the desired power at

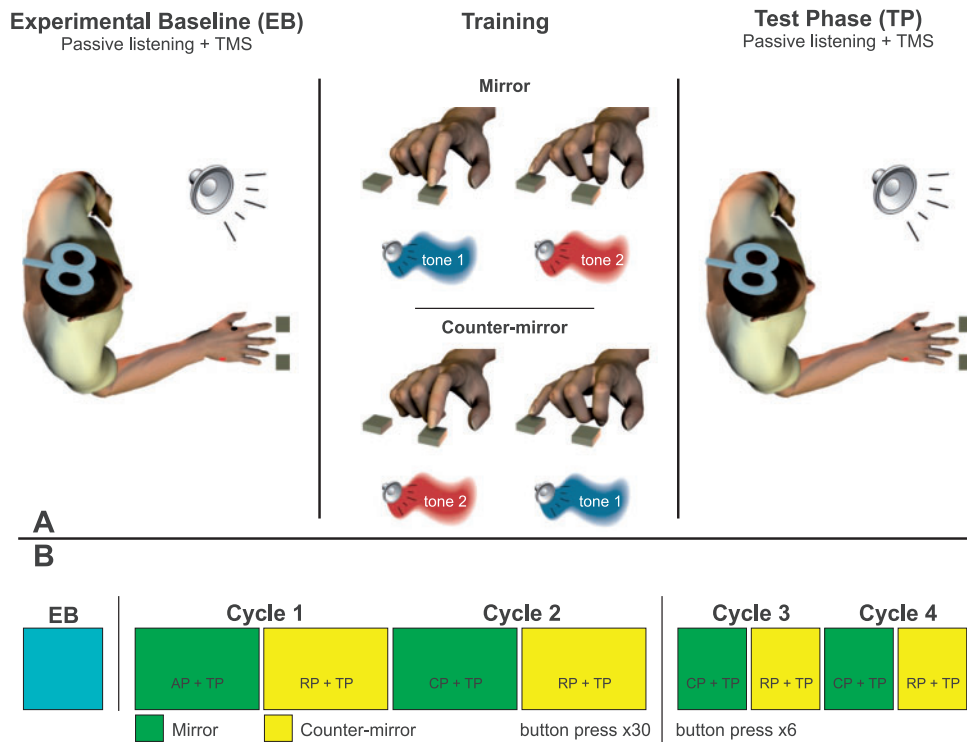


Fig. 1. (A) Illustration of the Experiment. In the Experimental Baseline (EB) and in Test Phases (TP), MEPs were recorded from the muscles of the index and little fingers during passive listening to two tones of different pitch. In EB, we tested for the existence of pre-existing mirror responses. MEPs in TP were recorded to investigate the sound-related modulations in the listener's motor cortex associated with mirror and counter-mirror trainings, in which participants triggered the two tones by index and little finger button presses. The assignment of tones to each button was opposite in each training session of each Cycle and was counterbalanced across participants. (B) Timeline of the experiment. After EB, the first training of the first Cycle (Acquisition Phase or AP) was followed by a first Reversal Phase (RP). Then, in the second Cycle, participants trained the contingent association between two button presses and the tones in a series of Consolidation and Reversal Phases (CP and RP, respectively). In the first and second group of four Cycles the trainings consisted of 30 and 6 button presses per training, respectively.

0.80. Participants were naive to the purpose of the experiment. They seated comfortably in the experimental room with the forearms on a table. Their right hand was positioned between two buttons (starting position), one located on the right side of the little finger and the other on the left side of the index finger (Figure 1A). They were asked to observe their hand throughout the experiment.

The experiment started with an Experimental Baseline (EB), in which we tested pre-existing mirror responses by recording motor-evoked potentials (MEPs) whilst participants passively listened to two tones of different pitch (MIDI tones of either 400 or 800 Hz, lasting 200 ms; SOA of 0 ms; instrument marimba; randomly presented binaurally through headphones 18 times each). Then four Cycles followed, each one composed of a mirror and a counter-mirror goal-directed training (see below), each followed by a Test Phase (TP; Figure 1A). During each training, the contingent association between two button presses and the tones (those already heard in EB) was learned. In TP, MEPs were acquired whilst participants passively listened to the tones presented 18 times in each training in random order to reduce anticipation effects. Notably, in each opposite training, the button-tone causal relationship was opposite to the preceding one and, consequently, participants executed opposite goal-directed 'mirror' and 'counter-mirror' trainings (Figure 1B). The first training of the first Cycle (Acquisition Phase or AP) was followed by a first Reversal Phase (RP). Consolidation (same training as in AP) and Reversal Phases (CP and RP, respectively) followed for a total of four Cycles (Figure 1B). During each training phase, participants performed free-choice button presses by abducting either the index finger (to press the left button) or

little finger (to press the right button) from the starting position in order to generate the tones. These movements maximised the activity of the FDI and the ADM muscles, respectively. In addition, two series of 16 MEPs each (baseline blocks) were recorded from each muscle at the beginning and at the end of the experiment, while participants kept their eyes closed.

We simultaneously recorded MEPs from FDI and ADM in response to single TMS pulses (Magstim 200, Whitland, UK) applied over each participant's right hand representation in the left primary motor cortex. Each pulse was randomly delivered at three different time intervals (50, 150 and 300 ms) from the onset of the tone, for a total of 36 MEPs in EB (equivalent to two Cycles of TP) and 144 MEPs in TPs from each muscle. In each training, the TMS pulses corresponding to the three time intervals were delivered three times for each of the two tones, for a total of 18 pulses for each training. The inter-stimulation interval was of 10–12 s. We used a 70 mm figure-of-eight stimulation coil positioned tangentially over the area of the lowest resting motor threshold (rMT, see below) with the handle oriented backward and laterally 45° away from the midline approximately perpendicular to the central sulcus. We set the intensity at 130% of each participant's rMT, defined as the lowest stimulator output sufficient to elicit five out of ten MEPs of $\geq 50 \mu\text{V}$ in the relaxed FDI. Electromyographic (EMG) signal was recorded with Ag-AgCl surface electrodes fixed on the skin with a belly-tendon montage, then amplified (gain: $\times 1000$), filtered (10–1000 Hz bandpass), digitised at 5 kHz (with a main hum notch filter at 50 Hz), displayed on the computer screen and finally stored for off-line analysis. No particular discomfort or negative side-effects were reported. In order to explore possible

variations of corticospinal excitability in relation to the number of trials trained in each training phase (see Introduction), participants executed thirty button presses in the first two Cycles and six button presses in the remaining two. Importantly, the assignment of tones (high vs low) to each button (left vs right) of the AP was randomised and counterbalanced across participants, and it was reversed at the transition between each consecutive training. In other words, for half of the participants, the high tone was associated with the left button and the low tone with the right one in the mirror training, whilst the high tone was associated with the right button and the low tone with the left one in the counter-mirror training. In the other half, the high tone was associated with the right button and the low tone with the left one in the mirror training, whilst the high tone was associated with the left button and the low tone with the right one in the counter-mirror training.

The result of the different muscle–tone combinations in TP was named ‘Tone 1’ and ‘Tone 2’: in Tone 1 condition the tone heard was the one previously associated (during AP or CP) with the muscle from which the MEP were recorded. In Tone 2 condition, the tone heard was the one associated with the opposite finger. Thus, in each TMS trial, one of the (simultaneously measured) muscles was associated with the presented tone, and the other was not (see also Ticini et al., 2012).

In each training, to assess the attention of the participant we introduced four catch trials (eight in EB) at a random time, in which the experimenter asked to the participant ‘Which tone have you just heard?’ (Answer: low/high).

Data analysis

Peak-to-peak MEP amplitudes were calculated as the absolute distance between the minimum and maximum values observed within a search window starting at 10 ms and ending at 80 ms after the TMS pulse. We discarded MEPs with detectable background activity preceding the TMS pulse in EB (0.5%), TP (2.5%), and in the two series of eight pulses at the beginning and at the end of the experiment (1.4%). Statistical analysis was performed using the standard tests of null hypothesis on mean MEP (collapsed across muscles, see Ticini et al., 2012) as dependent variable. We used the partial eta squared (η^2) to determine the effect size and set the alpha level at 0.05 for all statistical tests. When needed, we also computed Bayes Factors (BF_{10}) in JASP (Love et al., 2015), which allow to estimate the likelihood of the null hypothesis relative to the alternative hypothesis (Rouder et al., 2012). A $BF_{10} > 3$ indicates substantial evidence for the alternative hypothesis (Wetzels and Wagenmakers, 2012).

Results

The mean raw MEP amplitudes of the baseline blocks did not differ [one-way ANOVA: $F(1, 30) = 0.86$, $P = 0.36$]. Their average was therefore used to normalise the means values of each participant in each condition (therefore expressed as a percent change from the average of the baseline blocks).

The MEP recorded in EB for each tone (associated or not associated with the recorded muscle in the future muscle–tone combinations, respectively) were not different [$t(15) = 0.954$, $P = 0.36$; $BF_{10} = 0.38$], thus excluding that the auditory stimuli were associated with an action before the beginning of the experiment.

For TP, we run a repeated measures ANOVA with CYCLE (the four Cycles each containing a mirror and a counter-mirror training), TRAINING TYPE (goal-directed mirror training or counter-mirror training) and TONE (1 or 2, associated or not associated

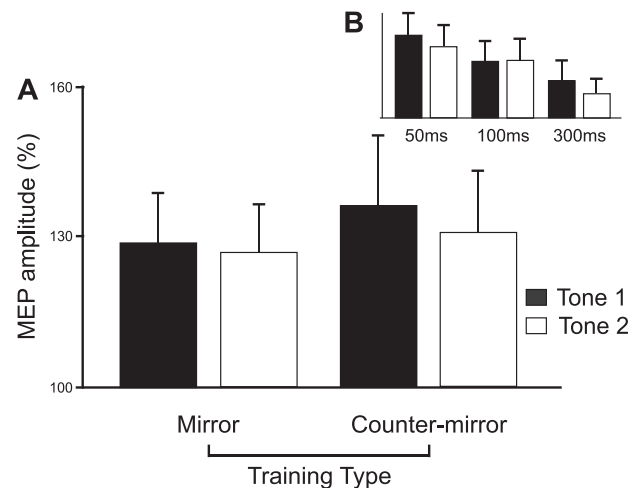


Fig. 2. (A) Modulation of mirror MEP amplitudes (mean \pm SE) recorded in TP during passive listening to the two tones. They are expressed as a percent change from the average of the baseline blocks. For clarity, the pattern of MEPs for the two training conditions (‘mirror’ and ‘counter-mirror’) is depicted separately. After the mirror training, MEPs were larger in response to the tone associated to each muscle during the training (Tone 1) when compared with MEPs triggered by listening to the other tone (Tone 2). A significant main effect of TONE ($P = 0.021$) and Bayesian analysis indicated that, in the counter-mirror experience, the same number of training trials that lead to the initial association did not suffice to reverse the MEP pattern. This result shows that voluntary goal-directed actions develop mirror MEP responses that, once acquired, are harder to reverse. (B) The MEP pattern for Tone 1 and Tone 2 at the three time points in which the TMS pulses were applied (50, 100, 300 ms after tone onset) is shown above the bars.

with the recorded muscle, respectively) as within-participants factors. The most relevant result was a significant main effect of TONE [$F(1, 15) = 6.63$, $P = 0.021$, $\eta^2 = 0.31$ (Figure 2)]. Whilst, the interactions TONE \times TRAINING TYPE [$F(1, 15) = 0.95$, $P = 0.35$, $\eta^2 = 0.06$] and CYCLE \times TONE \times TRAINING TYPE [$F(1, 15) = 0.79$, $P = 0.50$, $\eta^2 = 0.05$] were not significant. No other effects were found [$F_s < 1.8$, $P_s > 0.17$]. A Bayesian repeated measures ANOVA (Love et al., 2015) with default prior scales revealed that the main effects model of TONE was preferred to the interaction model TONE \times TRAINING TYPE by a BF of 16.6. This approach provided further evidence against the hypothesis of an interaction between the factors TONE and TRAINING TYPE.

This outcome indicates that a mirror-like effect was achieved with the mirror training, with larger MEP amplitudes in the Tone 1 condition when compared with Tone 2 one (Table 1). Importantly, we interpret the lack of a significant interaction TONE \times TRAINING TYPE as evidence that the counter-mirror training did not alter the initial association: indeed, mean MEP values were again larger for Tone 1 when compared with Tone 2.

We therefore conclude that, overall, the counter-mirror experience was unable to change the pattern of newly-developed MEP responses associated with the mirror trainings. If this were the case, then the MEPs recorded for Tone 2 after the counter-mirror trainings should have been larger than those for Tone 1. This was not the case.

In an exploratory attempt, we further tested whether the pattern of MEP differed at the three time points in which the TMS pulses were applied (see Cavallo et al., 2013; Barchiesi and Cattaneo, 2013). To do so, we run a repeated measures ANOVA with TONE, TRAINING and PULSE (50, 100, 300 ms after tone onset) as within-participants factors. The result indicated that the factors PULSE [$F(2, 30) = 14.4$, $P < 0.001$, $\eta^2 = 0.49$] and TONE

Table 1. Raw mean MEPs amplitudes \pm standard errors for the two tones in each Cycle and training condition (M = mirror training, CM = counter-mirror training)

Cycle	1		2		3		4	
	M	CM	M	CM	M	CM	M	CM
Tone 1	1.40 \pm 0.26	1.35 \pm 0.26	1.30 \pm 0.21	1.36 \pm 0.29	1.39 \pm 0.22	1.54 \pm 0.28	1.50 \pm 0.27	1.63 \pm 0.29
Tone 2	1.36 \pm 0.26	1.25 \pm 0.23	1.24 \pm 0.21	1.37 \pm 0.27	1.47 \pm 0.23	1.53 \pm 0.29	1.40 \pm 0.25	1.54 \pm 0.27

[$F(1, 15) = 6.51, P = 0.022, \eta^2 = 0.30$] were statistically significant. This again showed that MEPs for Tone 1 were larger than those for Tone 2, and that MEPs at 50ms were overall larger than those at 100ms, which were in turn larger than those at 300ms. Other main effects and interactions were not significant [$F_s < 0.9, P_s > 0.38$].

Discussion

We used a two-action/two-muscle design (in which recordings were made from two muscles executing two actions) to elucidate whether, in adult participants, newly learnt auditory mirror MEPs resist to an opposite and equivalent training. To the best of our knowledge, this is the first study directly comparing MEPs recorded after goal-directed 'mirror' trainings with those after goal-directed 'counter-mirror' trainings. The main finding is that counter-mirror experience could not reverse the newly-generated pattern of MEP responses, once self-executed actions were casually associated with arbitrary audible effects.

It is worth noting that in our experimental approach the participants developed mirror MEP responses *ex novo*. By selecting arbitrary tones that had no previous motor, verbal or semantic meaning (as demonstrated by the lack of significant effects in EB) we obtained comparable mirror and counter-mirror trainings. Contrarily, the classical associative counter-mirror approach aimed at modifying pre-existent mirror responses [either acquired through a lifelong sensorimotor experience (see Heyes, 2001; Hommel *et al.*, 2001; Keyser and Perrett, 2004) or potentially genetically pre-determined (e.g. Gallese and Goldman, 1998; Taschereau-Dumouchel *et al.*, 2016)] by means of contingent (and not causal) associations (e.g. Catmur *et al.*, 2007). Thus the two methods are completely different [but see the results recently obtained by Catmur and Heyes (2017) indicating that sensorimotor learning may also modulate imitation of goal-directed actions].

The experiment consisted of eight training sessions organised in four Cycles (Figure 1) in which participants generated two tones of different pitch, by performing free-choice button presses with the index and little fingers. Each training session presented buttons-tones contingencies that were opposite in respect to the preceding one (hence 'mirror' and 'counter-mirror' trainings). In other words, in each successive training the motor-sensory experience was reversed. After each training, we recorded MEPs from the index and little fingers' muscles in response to passive listening to the tones. The results showed that, irrespective of the counter-mirror experience, the tones continued to facilitate the muscles that generated them during the mirror training (Figure 2A). In particular, when the tone heard was that generated by the recorded muscle in the initial (mirror) training (Tone 1), the mean MEP size was larger than that recorded when listening to the other tone (Tone 2). After the counter-mirror training, the sound-muscle association remained unchanged, so that, from the perspective of the reversed training, larger mean MEPs were now measures for the

tone that was incongruent to the muscle according to the reversed training regime.

The fact that a short goal-directed training sufficed to establish a stable audio-motor association (as measured by a significant facilitation of the motor program necessary to produce a sound upon hearing that sound), and that the same number of trials failed to alter this association during the RP (as evidenced by our Bayesian analysis), constrains our understanding of the mirror neuron system by showing that this system is endowed with a mechanism that protects it against noise in the environment once established. The brain has a fundamental ability to extract knowledge about the permanent features and causal relationships that characterise our world: in our case, the properties of the experimental setup. This mechanism is advantageous as it allows to cope with situations without re-learning every time the most appropriate course of action. As the representation of action-goals in the brain must be of a high-order and stable character it could be argued that, as the mirror neurons code for action-goals (e.g. Fogassi, 2014), their response should also not be too malleable to experience.

On the one hand, this is in agreement with our previous TMS research (Ticini *et al.*, 2012) in which we demonstrated that a goal-directed training quickly develops stable representation of the goal of a motor act (the button-tone causal contingency of pressing a button to generate a specific tone), which is independent from the specific movements that were trained beforehand. Similarly, behavioural studies found that the auditory effects of voluntary actions become associated with the sensory representation of the button-tone (the goal of the action) rather than being associated with the representation of the movement (Hoffmann *et al.*, 2009), and that goal-directed actions are shifted in time towards their effects (Waszak *et al.*, 2005).

On the other, the outcome of our work argues against extreme views about the mirror-neuron system that hold that this system is so volatile in its representations that it cannot serve a direct-matching purpose (e.g. Catmur *et al.*, 2007). Why is it so? Below, we will highlight some features differentiating between goal-directed and associative learning as well as between goal-directed and goal-free (i.e. devoid of a target or goal, such as finger abductions) motor representations. Our aim is to indicate the reasons why sensorimotor representations of goal-free actions can be temporarily overruled by opposite experience whilst the representations of goal-directed motor acts seem more stable. We will bring evidence suggesting that the neuro-anatomical pathway and underlying learning mechanisms investigated in the goal-directed and associative trainings are different and involve two different neurophysiological routes from perceptual to motor areas.

Some authors seem to argue that object-free movements, traditionally encountered in associative counter-mirror experiments, are not coded by the mirror system (Rizzolatti *et al.*, 1988; Alexander and Crutcher, 1990a,b; Kakei *et al.*, 1999, 2001; Umiltà *et al.*, 2008). Truly, Cattaneo *et al.* (2009) demonstrated that the human motor system represents action goals as well as

movements devoid of a goal (see also the work on object-free actions, such as communicative gestures by Ferrari et al., 2003 and pantomimed reaching movements by Kraskov et al., 2009). In their TMS experiment, they instructed the participants to observe another individual using two different pliers that required opposite movement (normal and reverse pliers) to reach the same goal (grasping an object). They found that when there was no goal in the observed behaviour, MEP amplitudes reflected the movements observed regardless of the pliers used. Instead, during the observation of goal-directed actions, the MEP pattern was modulated by the action goal (i.e. despite opposite hand movements necessary to obtain it).

We may wonder why our present and previous (Ticini et al., 2012) investigations suggest that the latter representation is less susceptible to reversal. Converging evidence demonstrates that only voluntary and goal-directed movements, in which there is causality between intentional actions and subsequent sensory effects, result in stronger sensorimotor learning (Herwig and Waszak, 2009; Herwig et al., 2007). As such, mirror responses may initially emerge when experiencing the causality (rather contingency as implied in the associative sequence learning hypothesis) between one own's self-executed actions and their perceivable consequences (Casile et al., 2011; Del Giudice et al., 2009; Heyes, 2001; Keyzers and Perrett, 2004; Keyzers et al., 2014). Also at the neuronal level, synaptic potentiation establishing a stable correspondence between action and perception only occurs when the pre-synaptic input precedes post-synaptic activity ('when one cell repeatedly assists in firing another'; Hebb, 1949), and when there is contingency and causality between an action and its sensory effects (Keyzers and Perrett, 2004; Keyzers et al., 2014). On the contrary, the associative learning account establishes that contiguity between a stimulus and an action (when neurons 'fire together'), occurring when participants learn to respond with an action to a preceding stimulus (stimulus–response learning; e.g. Brass and Muhle-Karbe, 2014), would suffice.

Last but not least, neuroimaging work demonstrated that stimulus–response and action–effect goal-directed learning are controlled by different neural substrates (e.g. Herwig et al., 2007; for a review of the work see also Waszak et al., 2005). For instance, Barchiesi and Cattaneo (2013) postulated that arbitrary association may involve brain areas such as the pre-frontal cortex (for its role in stimulus–response associations and in response selection under conflict; Mansouri et al., 2009; Ridderinkhof et al., 2010, respectively), the right inferior frontal gyrus or the anterior middle pre-frontal cortex (for their involvement in response inhibition; Aron et al., 2004; Brass et al., 2005). Instead, the neural substrate dedicated to coding for the goals of actions would involve a temporal–parietal–ventral pre-motor network of areas (Rizzolatti and Matelli, 2003; see also Melcher et al., 2008) already identified in neurophysiological studies in the animal brain (Umiltà et al., 2008; Kakei et al., 1999, 2001). As a matter of fact, in a TMS study, Ubaldi et al. (2015) found experimental evidence for a dual-route in the genesis of (fast) automatic mirror responses vs (slow, relying on higher-order motor areas such as the dorsolateral pre-frontal cortex) rule-based 'counter-mirror' responses cued by observed hand movements (akin to the work by Catmur et al., 2007). Further experiments are needed to corroborate our findings by directly comparing the effects of goal-directed (motor-sensory, in which the tone is causally generated by a movement) and associative (sensory-motor and contingent, in which the tone would precede the movement) counter-mirror training on mirror MEP responses.

Albeit notional, another result of our work suggests that the mirror-like modulation of the MEPs did not differ across the time points (main effect of TONE when considering MEPs at 50, 100 and 300 ms), and that MEP amplitudes were larger at earlier TMS delays (main effect of PULSE). This, on the one hand, may indicate that mirror responses were already present as early as 50 ms post-stimulus onset and, on the other, that the motor system reduced its contribution over time as the informative content of the stimulus decreased (became less salient or there was less uncertainty of discrimination; for a review of the timing of the mirror response, see Naish et al., 2014).

The classical organisation of the pathway involved in visuo-motor mirror activity indicates a 350 ms long process in which perceptual areas, the superior temporal sulcus, the inferior parietal lobule, inferior frontal gyrus and primary motor cortex are involved (Nishitani and Hari, 2000, 2002). Nonetheless, van Schie et al. (2008) reported a neuromagnetic readiness fields at 83 ms after movement onset during observation of goal-directed movements. Obviously, the nature of visual stimuli is quite different from ours, which were auditory, lasted only 200 ms and were not comparable to observed actions that gradually unfold over time (Gangitano et al., 2001). This difference may explain why the pattern of auditory mirror responses differed from those observed during action observation, that show early non-specific modulation of corticospinal excitability during action observation (Lepage et al., 2010b).

The auditory pathway is also faster than the visual pathway. Electrophysiological recordings in the monkey's ventral pre-motor cortex (Kohler et al., 2002) showed latencies in response to complex action-related sounds as short as 50 ms. In the human brain, action-related sounds can trigger motor cortex activity in both early (Hauk et al., 2006) and late (De Lucia et al., 2009; Pizzamiglio et al., 2005) time windows. For instance, Lepage et al. (2010a,b) revealed modulations for finger-clicks, when compared with control sounds, at 100 and 300 ms circa. This, according to the authors, called for a more direct route through subcortical-motor projections mapping action information in a crude manner. Furthermore, early auditory evoked potential to sounds were observed in a window between 50 and 150 ms in the auditory, parietal, motor and pre-motor cortices (Näätänen and Picton, 1987) and at 100 ms during speech perception (Roy et al., 2008). Early effects of the sound are in agreement with other experimental data on auditory-motor associations occurring very early after stimulus onset exactly in the 50 ms interval (Serino et al., 2009; Cattaneo and Barchiesi, 2015). Interestingly, as our MEP pattern was tone specific and taking place already at an early time onset, we can exclude the possibility that these were non-specific alerting effects (van Schie et al., 2008) or voluntary audio-motor responses (that would appear later than 100 ms from stimulus onset; Valls-Sole et al., 2008). Cattaneo and Barchiesi (2015) speculated that early corticospinal responses may require fast trans-cortical loops linking the temporal primary auditory cortex (reached by the auditory information at 30 ms from stimulus onset; Liegeois Chauvel et al., 1994) to the auditory maps in the parietal (Cohen and Andersen, 2002) and pre-motor cortices (Graziano et al., 1999). As an alternative, they also proposed a summation at the level of the spinal cord of convergent descending volleys independently evoked by auditory stimuli in the tecto-spinal tract, known to produce spatially-oriented behaviour, and the motor neurons (activated by TMS around 56–58 ms from sound onset). Our experimental setup doesn't allow to exclude possible subcortical contributions of this kind and additional experiments

are needed to provide more cues on where these physiological signals originate from.

Finally, our results indicate that the first kind of auditory-motor associations tends to become stable and consolidated into a protected state in a ‘first come—first serve’ manner, as in the consolidation theory of motor memory (Krakauer and Shadmehr, 2006). This theory, albeit widely challenged (see for example Caithness et al., 2004), suggests that motor memories of a task are lost when an opposing task is trained soon after but, if sufficient time is allowed to pass (10 min to 6 h), they may undergo a first stage of consolidation where they are stabilised against interfering new learning (e.g. Walker et al., 2003). It is thought that further consolidation occurs during sleep (e.g. Walker et al., 2002; but see also Brawn et al., 2010), and that the stabilisation of motor memories engages separate brain areas (Albert et al., 2009): in particular, cognitively challenging practice would involve the dorsolateral pre-frontal cortex whilst less demanding tasks would require the motor cortex (Kantak et al., 2010). Evidence also indicated that explicit and implicit motor learning work differently (but for an opposing view, see Willingham and Goedert-Eschmann, 1999). Indeed, practicing a motor task with awareness of what is being learned would require a period of sleep (Robertson et al., 2004), whilst a wakeful period following practice is sufficient to consolidate motor memories when there is little or no awareness of task features (Robertson et al., 2005).

Knowledge about memory consolidation might inform us about the mechanisms differentiating automatic mirror (as in our experiment) from rule-based counter-mirror responses (required in associative counter-mirror experiments). For instance, as shown by Ubaldi et al. (2015), the latter learning involves the dorsolateral pre-frontal cortex as in the case of motor memories associated with cognitively challenging practice. Moreover, we described an experiment in which the opposite learnings followed each other continuously, while tests in associative experiments were conducted 24 h after training (Catmur et al., 2007) or over the course of consecutive days (Catmur et al., 2008) thus possibly allowing for a different kind of consolidation of the novel motor state. In addition, participants to our experiment underwent an easy task in which the learning process was implicit whilst the associative experimental settings required more explicit rule-based learning processes. This, again, suggests that the motor training and consolidation underneath the two kind of experiments are likely to be different in many different aspects.

In conclusion, our result demonstrates that the execution of voluntary goal-directed actions develops auditory-motor associations that, once acquired, are harder to reverse with further sensorimotor experience. It also establishes the principle that a minimum quantity of equivalent counter-mirror experience is not sufficient to reverse the pattern of newly-formed mirror MEPs.

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