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Eliminating mirror responses by instructions

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ABSTRACT

The observation of an action leads to the activation of the corresponding motor plan in the observer. This phenomenon of motor resonance has an important role in social interaction, promoting imitation, learning and action understanding. However, mirror responses not always have a positive impact on our behavior. An automatic tendency to imitate others can introduce interference in action execution and non-imitative or opposite responses have an advantage in some contexts. Previous studies suggest that mirror tendencies can be suppressed after extensive practice or in complementary joint action situations revealing that mirror responses are more flexible than previously thought. The aim of the present study was to gain insight into the mechanisms that allow response flexibility of motor mirroring. Here we show that the mere instruction of a counter-imitative mapping changes mirror responses as indexed by motor evoked potentials (MEPs) enhancement induced by transcranial magnetic stimulation (TMS). Importantly, mirror activation was measured while participants were passively watching finger movements, without having the opportunity to execute the task. This result suggests that the implementation of task instructions activates stimulus-response association that can overwrite the mirror representations. Our outcome reveals one of the crucial mechanisms that might allow flexible adjustments of mirror responses in different contexts. The implications of this outcome are discussed.

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1. Introduction

There is ample evidence that the observation of an action leads to the activation of the corresponding motor plan in the observer (Blakemore & Frith, 2005; Brass, Bekkering, & Prinz, 2001; Brass & Heyes, 2005; Cook, Bird, Catmur, Press, & Heyes, 2014; Gazzola & Keiser, 2009; Grèzes & Decety, 2001; Heyes, 2011; Keysers & Gazzola, 2010; Massen & Prinz, 2009). Support for such a direct matching mechanism was provided by behavioral studies (Brass et al., 2001; Craighero, Bello, Fadiga, & Rizzolatti, 2002; Kilner, Paulignan, & Blakemore, 2003),

single-cell recordings in monkeys (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992), functional fMRI (Gazzola & Keiser, 2009; Keiser & Gazzola, 2010) and motor TMS (Catmur, Walsh, & Heyes, 2007; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). It was claimed that such a ‘mirror mechanism’ forms the basis for imitation, action understanding and social cognition (Bastiaansen, Thioux, & Keysers, 2009; Brass & Heyes, 2005; Cook et al., 2014; Gallese, 2003; Gallese & Goldman, 1998; Hurley, 2008; Rizzolatti & Craighero, 2004). Alternatively, it has been argued that mirror representations are simply a byproduct of motor control and

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not necessarily play a role in social cognition (Brass & Heyes, 2005; Cook et al., 2014).

However, mirror responses are not always beneficial for successful behavior. An automatic tendency to imitate others can introduce interference in action execution when the observed action is different from the response that needs to be performed (Brass et al., 2001; Craighero et al., 2002; Kilner et al., 2003). Moreover, non-imitative responses have an advantage in some contexts, such as when complementary, rather than identical, actions need to be executed in joint action tasks (Sebanz, Bekkering, & Knoblich, 2006; van Schie, van Waterschoot, & Bekkering, 2008).

A recent body of evidence suggests that mirror tendencies are not unavoidable. Relatively brief periods of sensorimotor experience can enhance (Press, Gillmeister, & Heyes, 2007; Wiggett, Hudson, Tipper, & Downing, 2011), abolish (Cook, Press, Dickinson, & Heyes, 2010; Gillmeister, Catmur, Liepelt, Brass, & Heyes, 2008; Heyes, Bird, Johnson, & Haggard, 2005) or reverse (Catmur, Mars, Rushworth, & Heyes, 2011; Catmur et al., 2008, 2007; Cavallo, Heyes, Becchio, Bird, & Catmur, 2014) mirror responses. For example, 90 min of incompatible sensorimotor training in which participants are instructed to make an index finger movement while observing a little finger movement, and vice versa, is sufficient to reverse the pattern of motor evoked potentials (MEPs) after a TMS pulse: the observation of index finger movements elicit more activity in the little finger muscle than observation of little finger movements (Catmur et al., 2007). According to the associative sequence learning (ASL) theory (Heyes, 2001), perception-action links mediating mirror responses arise primarily through correlated experience of observing and executing the same actions (Cook et al., 2014; de Klerk, Johnson, Heyes, & Southgate, 2015; Ray & Heyes, 2011). Consequently, a visuo-motor training with incompatible mappings directly affects the mirror system, which can acquire counter-mirror properties (Catmur et al., 2007; Heyes et al., 2005).

A reversal of mirror tendencies was also found in the context of complementary actions, both at the behavioral (Newman-Norlund, van Schie, van Zuijlen, & Bekkering, 2007; van Schie et al., 2008) and physiological level (Barchiesi & Cattaneo, 2013; Sartori, Buccioni, & Castiello, 2013; see also Hamilton, 2013). In the study of Sartori, Betti, and Castiello (2013) and Sartori, Buccioni, et al. (2013), participants watched videos of action sequences while MEPs were recorded from finger muscles. The videos showed an actor pouring coffee (whole hand grasp) or sugar (precision grip) into espresso cups. At the beginning of the video, the MEP pattern indicated mirroring: when observing a whole hand grasp, participants showed a large MEP both in the index and little finger muscles (both muscles are recruited for a whole hand grasp). However, when the model moved as if she wanted to pour coffee into an espresso cup which was located close to the participant, only the FDI muscle (needed to perform a precision grip) was activated, suggesting that participants implicitly prepared to perform a reciprocal action: pick up the cup and offer it to the actor. This outcome suggests that the system is able to rapidly switch from mirroring to complementarity as a function of social context.

Taken together, recent evidence suggests that imitation and direct visuo-motor matching could be more flexible than

previously thought. However, the mechanisms underlying these modulation effects are still poorly understood.

In the area of complementary actions, response flexibility has been suggested to be realized by different population of mirror neurons: strictly congruent ones, which are activated when the observed action and the one that is executed are identical, and broadly congruent ones, which are activated when the context calls for a nonidentical (e.g., complementary) action with the same common goal. The mirror system would therefore govern response flexibility to activate different types of actions dependent on social interaction (Newman-Norlund et al., 2007; van Schie et al., 2008). However, how the mirror system is informed about the context is still poorly understood. It has been suggested that the flexible integration of observation and execution needed in joint-actions recruits mechanisms outside the mirror system (Barchiesi & Cattaneo, 2013; Kokal, Gazzola, & Keysers, 2009; see also Sartori, Betti, et al., 2013 for discussion).

Further support for the idea that flexibility of mirror responses may employ general mechanisms comes from Barchiesi and Cattaneo (2013). These authors suggest that the visuo-motor matching of mirror neurons can be changed by recent experiences only to a limited extent, without reversing it. In this study, the kinematic of TMS-evoked movements was recorded after imitative and counter-imitative training. Before training, the movement kinematics mirrored the observed action when TMS was delivered 250 and 320 msec after stimulus onset. After counter-mirror training, responses at 250 msec were unchanged and still mirrored the stimuli. Training-dependent changes in evoked responses were observed only at 320 msec. On the basis of the different time courses of mirror and counter-mirror response activations the authors suggested a dual-route model. Here, distinct mechanisms would mediate imitative responses and action tendencies related to recently learned stimulus-response mappings.

On the basis of these results the question arises how flexibility of mirror responses is realized. Do these manipulations affect the mirror system as such or create new stimulus-response (S-R) associations that dominate mirror representations?

Interestingly, outside the domain of social cognition, many studies have shown the ability of humans to flexibly learn arbitrary S-R relations, where learned or instructed relations strongly affect the selection of future responses (e.g., Hedge & Marsh, 1975; Hommel, 1993; Marini, Iani, Nicoletti, & Rubichi, 2011; Ottoboni, Iani, Tessari, & Rubichi, 2013; Proctor & Lu, 1999; Proctor, Yamaguchi, Dutt, & Gonzalez, 2013; Tagliabue, Zorzi, Umiltà, & Bassignani, 2000; Theeuwes, Liefoghe, & De Houwer, 2014; Vu and Proctor, 2004). Recently, it has been shown that the mere instruction of a stimulus-response mapping can induce automatic response tendencies in a completely unrelated task (Liefoghe, De Houwer, & Wenke, 2013; Liefoghe, Wenke, & De Houwer, 2012; Theeuwes et al., 2014). Interestingly, instructions are even strong enough to counteract automatic response tendencies based on long-term S-R links, as in the Simon task (Theeuwes et al., 2014). The same effect was previously obtained with practice (Proctor & Lu, 1999; Tagliabue et al., 2000). Importantly, instructions-based and practice effects have been attributed to the implementation of short-term S-R associations, which

overwrite the effect of automatic response tendencies, influencing performance in the following task (Proctor & Lu, 1999; Proctor et al., 2013; Tagliabue et al., 2000).

In the current study, we took advantage of task instruction procedures to investigate whether instructions are sufficient to realize response flexibility. In detail, we sought to test whether direct matching of an observed action onto a corresponding motor representation can be eliminated based on mere task instructions, in the absence of contextual manipulations or sensorimotor learning. Such results would demonstrate that response flexibility can be implemented without directly affecting the mirror system, because it is very unlikely that verbal instructions alone modify the mirror system. A hand performing an index or a little finger movement was presented on a computer screen. Participants received either compatible (i.e., respond by performing the same movement) or incompatible instructions (i.e., respond by performing the opposite movement) at the beginning of two sessions. Before task execution, participants were asked to passively observe the stimuli while we applied TMS to the primary motor cortex and recorded the MEPs from the participant's index and little finger muscles. In the baseline session (compatible instructions) we expect to observe a mirror pattern, which is a muscle-specific enhancement of corticospinal excitability in response to finger stimuli. More importantly, if the mere presentation of counter-mirror instructions is sufficient to counteract the activation of the mirror system, we expect differences in corticospinal excitability to be reduced in the second session (counter-mirror instructions). On the contrary if rapid switch in response activation from mirror to different action is governed by the mirror system and can be only driven by social interaction or sensorimotor learning, the mere presentation of task instructions should not be sufficient to induce changes in corticospinal excitability.

2. Methods

2.1. Participants

Thirty right-handed healthy young adult men (mean age = 22.3 years) took part in this study and signed the informed consent in accordance with the declaration of Helsinki from 1964. Three participants were excluded from the final sample because they did not follow the instructions correctly (they gave responses during passive observation trials) or due to problems in saving EMG data. Participants were paid for their participation in this experiment (25 euros). Thus, the final sample included 27 participants. They had no history of neurological or psychiatric disorders, had normal or corrected-to-normal vision and were prescreened for the risk factors associated with TMS (Rossi, Hallett, Rossini, & Pascual-Leone, 2009). The study was granted ethical approval by the Medical Ethical Review Board of Ghent University Hospital.

2.2. TMS stimulation and MEP recording

Electromyographical (EMG) activity was recorded with the ActiveTwo system (BioSemi). Sintered 11×17 mm active Ag–AgCl electrodes were placed over the right first dorsal

interosseus (FDI) and right abductor digiti minimi (ADM). These muscles contribute to abduct the index finger away from the middle finger and the little finger away from the ring finger, respectively. The active electrodes were placed over the belly of the right FDI and ADM muscles and the reference electrodes over the ipsilateral proximal interphalangeal joints (belly-tendon montage). The ground electrode was placed on the back of the hand, near the wrist joint. EMG signal was amplified (internal gain scaling), digitized at 2 kHz, high-pass filtered at 3 Hz, and stored on a PC for offline analysis. TMS pulses were delivered by a biphasic magnetic stimulator (Rapid2; Magstim). A 70 mm figure of eight coil was held tangentially to the skull with the handle pointing backward and laterally at a 45° angle to the sagittal plane. The coil was positioned in correspondence with the optical scalp position defined as the coil position eliciting the largest and more reliable MEPs in both the FDI and the ADM. The stimulation intensity was determined based on the resting motor threshold (rMT) of both muscles, which is defined as the intensity that evokes an MEP larger than 50 μ V in 50% of the cases (Rossini et al., 1994) in the FDI and ADM simultaneously. Participants were equipped with a swimming cap on which the optimal location for stimulation was marked so that the experimenter could easily track the correct position of the coil during the experiment. During the experiment, a mechanical arm held the TMS coil. Experimenters continuously monitored the coil position during the sessions. Stimulation intensity during the recording session was set to 110% of the rMT. Average intensity was 73.2% (range 55%–79%) of the maximal stimulator output.

2.3. Stimuli and procedure

Participants seated in a comfortable armchair in front of a computer monitor in a dimly lit room. The participant's right arm was placed in a horizontal orientation across their body, controlling for both simple and orthogonal spatial compatibility between the participant's hand and the stimulus hand (Fig. 1). The tips of the index and little finger were placed on a response box with light-sensitive sensors. Experimental stimuli were presented on a 17-inch computer monitor (1024×768 pixels) via Eprime Software 2.0 (Psychology Software Tools, PA, USA). The trial sequence was based closely on Catmur et al. (2007). At the beginning of a trial a fixation cross was presented centrally on the screen for 1000 msec. Stimuli were sequence of two images of a hand (height: 12° of visual angle, width 6° of visual angle). Each sequence consisted of an image of the dorsal view of a static hand, presented for a variable time interval (800, 1600, or 2400 msec), and this was followed by an image of one of two end postures: index–finger abduction and little-finger abduction, which was presented for 960 msec. This succession of images produced apparent motion. At a variable interval (200, 250, or 320 msec) from the onset of the end-posture stimulus, the TMS pulse was triggered.

Each task session consisted of 144 trials, divided in 4 blocks (36 trials each). In each block, 18 index and 18 little finger abduction movements were presented in a random order. At the end of the first session (baseline session), participants were given a 5 min break. The experiment lasted about 1.20 h in total.

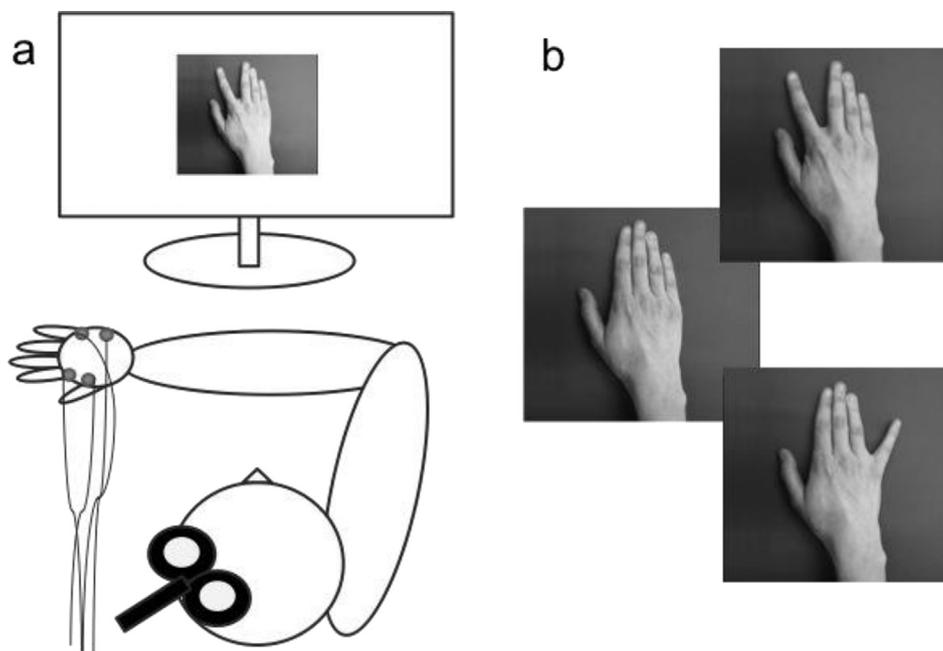


Fig. 1 – (a) Schematic drawing of the experimental setup. The participant's right arm was placed in a horizontal orientation across their body, controlling for spatial compatibility between the participant's hand and the stimulus hand presented on the screen. TMS was applied to the left M1 and EMG activity was recorded from the index and the little finger of the participant's right hand. (b) The stimulus frames. To create the apparent finger movement, a static frame depicting either the end point of index finger abduction or the end point of a little finger abduction followed a static hand frame.

2.4. Baseline session

At the beginning of first session, two instruction screens were presented. First, participants were instructed to make an abduction of their index finger as soon as they saw the index finger movement and to abduct their little finger as soon as they saw the little finger movement. With the second screen, participants were told that they would have been asked to perform the task later, after trials of passive observation of the stimuli on the screen. Crucially, they did not perform any kind of movement during four blocks of stimuli presentation. However, to ensure the engagement of participants in the task, they were explicitly told that the actual task could be introduced at any time and therefore it was necessary to keep the instructions in mind. After each block, participants were asked to keep in mind the instructions. After four experimental blocks in which participants only observed the stimuli, an instruction screen was given asking participants to perform the instructions they received at the beginning of the session. Twelve additional stimuli were presented. Stimuli were identical to the ones presented in the baseline session. Here participants responded by making an abduction of their index finger when an index finger abduction was presented on the screen and by making an abduction of their little finger when a little finger abduction was presented. Behavioral and EMG data were collected during task execution. Data analysis revealed that all participants included in the final sample correctly executed the task. These data were not considered any further.

2.5. Counter-mirror session

The counter-mirror session was identical to the baseline session except for the instructions that participants received at the beginning of the session. Here, participants were asked to respond with the opposite finger movement relative to the movement presented on the screen: they were instructed to make an abduction of their index finger as soon as they saw the little finger movement and to abduct their little finger as soon as they saw the index finger movement. As well as in the baseline session, participants were required to keep in mind the instructions and only observe the stimuli on the screen because the actual task could be introduced at any time. Although the participants were told that the actual task would have been introduced at some point, the task was omitted at the end of the session because it was irrelevant to the purpose of the current study.

2.6. Data analysis

For each TMS trial, the peak-to-peak amplitude of the MEP was calculated. This was done by extracting the epochs starting 500 msec before and after the actual event (i.e., the TMS pulse) from the recorded data. Data were checked for background EMG activity during a time window of 500 msec preceding the TMS pulse and if this was found, the data for this trial were rejected. The peak-to-peak amplitude of each trial was calculated for the 20–50 msec window following an event (i.e., the typical time range at which an MEP occurs) and MEPs were

computed using MATLAB® software. Individual trials with amplitude of at least 50 μV were averaged per participant, session, muscle and stimulus. Data were transformed to normality by a log-10 distribution. The Kolmogorov–Smirnov test confirmed that the transformed data were normally distributed. To confirm the presence of a muscle-specific action observation effect in the baseline session, we entered data into a repeated-measures analysis of variance (ANOVA) with two within-subjects factors: recorded muscle (FDI, ADM) and observed movement (index–finger abduction, little–finger abduction). To investigate the effects of instructions, we entered data from both sessions into an ANOVA with session (baseline session, counter-mirror session) muscle, and observed movement as within-subject factors. Post-hoc comparisons with Bonferroni correction were performed on the significant interactions.

3. Results

The presence of a muscle-specific mirror effect in the baseline session was confirmed by a significant interaction between muscle and observed movement [$F(1,26) = 10.89, p < .01, \eta^2 = .29$]. More interesting, the ANOVA including the two sessions, revealed a significant interaction of muscle, observed movement and session [$F(1,26) = 11.23, p < .01, \eta^2 = .30$]. Following the same procedure adopted by Catmur et al. (2007), we then selected 15 participants who showed the clearest mirror effect in the baseline, with substantial muscle-specific enhancement of MEPs in both muscles and performed the following analyses on this sample.

The ANOVA including session, muscle and observed movement as within-subjects factors revealed a significant interaction of muscle, observed movement and session [$F(1,14) = 21.34, p < .01, \eta^2 = .60$]. In the baseline session, the FDI muscle showed higher MEP amplitude for the observation of the index finger movement than for the observation of the little finger movement ($p < .01$). The ADM muscle showed the reverse pattern with higher MEP amplitude for little finger stimulus than for index finger stimulus ($p < .01$). In the counter-mirror session these differences were suppressed ($ps > .01$) (Fig. 2).

Finally, since one may argue that the effect of the session is due to habituation or fatigue, we measured the mirror effect across time during both sessions. For this analysis, each session was divided in two halves (due to the small number of trials per block, data from block 1 and block 2 and data from block 3 and 4 were averaged) and an ANOVA with session, half, observed movement and muscle was performed. Results revealed a significant interaction of session, muscle and observed movement [$F(1,14) = 20.38, p < .01, \eta^2 = .59$]. Moreover, the interaction of session, half, muscle and observed movement approached significance [$F(1,14) = 4.57, p = .05, \eta^2 = .25$] (Fig. 3). In the first session, a significant mirror pattern was confirmed both in half 1 and 2 for FDI and ADM muscles (index finger stimulus vs little finger stimulus for FDI and vice versa for ADM, $ps < .01$). However, the FDI muscle showed a higher difference in the second half (index finger stimulus minus little finger stimulus in half 1 vs index finger stimulus minus little finger stimulus in half 2, $p < .05$). In the

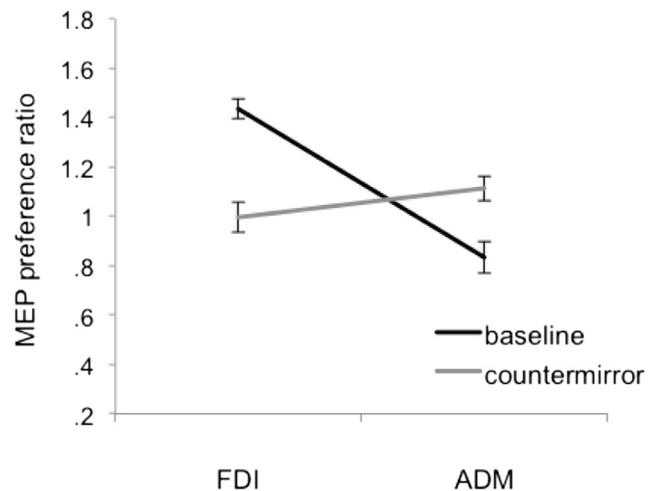


Fig. 2 – The graph shows the effect of instructions (15 participants). For illustration purposes, MEP preference ratios are shown. MEP ratios were calculated in the following way: for both FDI and ADM muscle, mean MEP size during observation of index finger movement divided by the mean MEP size during observation of little finger movement. The ratio represents the degree to which MEPs recorded in the muscle were larger for index than for little finger movement observation. A mirror effect is indicated by higher value in the FDI than in the ADM muscle. In the baseline session, the observation of the index finger induced higher activation in the FDI than in the ADM muscle whereas a reversal of this pattern was observed after counter-mirror instructions.

second session, the mirror pattern was suppressed in both FDI and ADM muscle ($ps > .05$). No differences between half 1 and 2 were detected in the second session. Fig. 3 demonstrates that the mirror effects shows no sign of reduction in the first session and hence renders habituation or fatigue an unlikely explanation for our effects.

4. Discussion

The aim of the present study was to investigate whether automatic ‘mirror responses’ can be eliminated through verbal instructions only. Here we show that the mere instruction of a counter-imitative mapping changes mirror responses at the neurophysiological level, as indexed by MEPs enhancement. Importantly, these mirror responses were measured while participants were passively watching finger movements. This finding has important theoretical implications regarding the power of verbal instructions as well as regarding potential mechanisms underlying counter-mirror responses in previous work. While the modification of automatic S-R links has already been described in the context of spatial compatibility, our study is the first that demonstrates that instructions can also overrule imitative response tendencies. This finding along with previous research on spatial compatibility cast doubts on the idea that counter-mirror effects

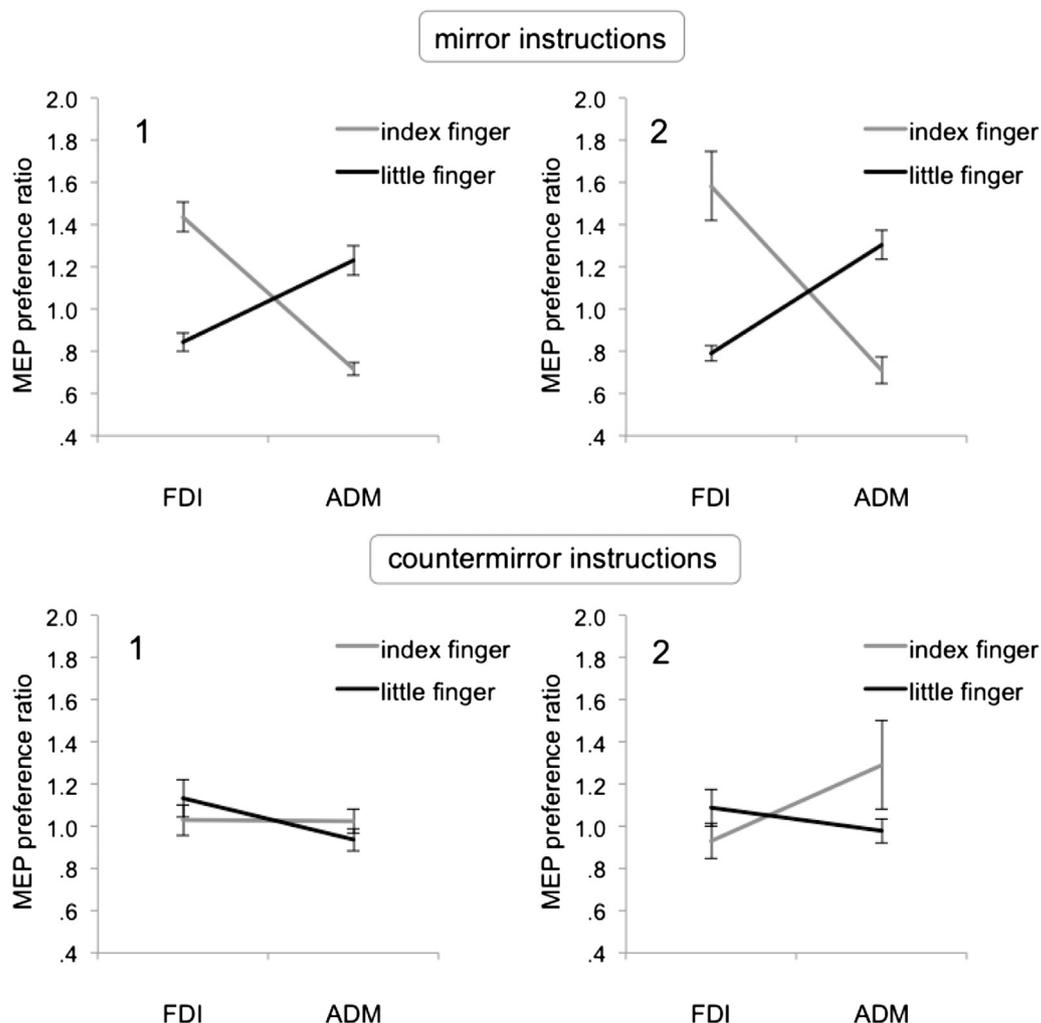


Fig. 3 – The graph represents MEP ratios for the FDI (index finger) and the ADM (little finger) muscles during the first and the second sessions (15 participants). Here MEP ratios are represented both for index finger stimuli (observing index/observing little) and little finger stimuli (observing little/observing index). Upper panel: first half (panel 1) and second half (panel 2) of the first session. MEP preference ratios show that, for each muscle, MEPs are higher during observation of the corresponding finger stimulus. Lower panel: first half (panel 1) and second half of the second session (panel 2).

might reflect a rewiring of the mirror system. Rather they suggest that S-R instructions and fast S-R learning creates strong S-R links that overshadow existing ideomotor associations.

In the context of spatial compatibility effects, many studies have shown the ability of humans to flexibly learn arbitrary S-R relations, where learned or instructed relations strongly affect the selection of future responses (e.g., Hedge & Marsh, 1975; Hommel, 1993; Marini et al., 2011; Ottoboni et al., 2013; Proctor & Lu, 1999; Proctor et al., 2013; Tagliabue et al., 2000; Theeuwes et al., 2014). However, research on imitation has mostly focused on the unavoidable coupling between perception and action (Fadiga, Craighero, & Olivier, 2005). Our results are in line with previous evidence that mirror responses can be modulated by practice or in the context of joint actions (e.g., Catmur et al., 2007; 2008; 2011; Heyes et al., 2005; van Schie et al., 2008). However, we go

far beyond showing that practice, or joint action contexts, are not necessary.

To explain the elimination (and reversal) of the Simon effect after practice with spatial compatibility task with incompatible mapping, Tagliabue et al. (2000) introduced the notion of “long-lasting short-term links.” According to their computational model, when practicing a spatially incompatible task, short-term (task-related) associations between a stimulus location and the incompatible response are created in order to perform the spatial compatibility task. This links remain active and influence performance in the subsequent Simon task. When a stimulus with a given spatial code occurs, the response that has been associated with it by practice is retrieved automatically, thereby influencing performance. Although the fashion of how task instructions are translated into actions is still a matter of debate (for a review see Meiran, Cole, & Braver, 2012), instructions effects have been

interpreted in a similar way: S-R mappings are implemented into S-R associations, which trigger responses even when the mapping is irrelevant for the current task (instruction-based response activations; De Houwer et al., 2005). What is important here is that new S-R links produce effects that cover up automatic response activation but neither practice nor instruction-based effects are thought to directly modify or suppress long-term associations, which are considered being unmodifiable (Proctor et al., 2013; Tagliabue et al., 2000; Theeuwes et al., 2014). Our results reveal that a similar mechanism can be applied to the mirror system.

This is in line with what was proposed in the study of Barchiesi and Cattaneo (2013). Thanks to the analysis of the time course of mirror and counter-mirror response tendencies in the same trial, these authors suggest that training with counter-mirror response mapping is not able to reverse mirror response. Instead, the mirror system would remain active shortly after stimulus presentation and is covered up by arbitrary S-R mapping only at a later timing. Direct visuo-motor transformation underlying mirror response and recently learned S-R mappings would be mediated by two different routes of information processing.

The idea that mirror responses can be modulated by general mechanisms does not contradict the notion that spatial compatibility and mirror compatibility have different properties and therefore are based on different mechanisms (Catmur & Heyes, 2011) but suggests that the way response flexibility is applied to the mirror system can be similar. Although shared representations can be considered as a default mode of brain function, when the instructions/context call for a different action, task specific short-term S-R relations between the observed virtual behavior and the response selected by the subject can temporarily cover up mirror links so that visuo-motor associations can be quickly redefined. Importantly, this does not require extensive experience with new S-R mapping and does not necessarily imply changes in the inherent properties of the mirror system to be introduced (e.g., Catmur et al., 2007).

Our results do not speak against the associative learning idea of the origin of the mirror system, and let alone wants to deny the role of sensory-motor experience in shaping the mirror system and imitative behavior during the life span. However, it is also conceivable that the processes underlying explicit learning and instructions effects, which ensure high flexibility of the adult's cognitive system, are qualitatively different from those that forge the mirror system during the early phase of development (Wiggett et al., 2011). From an ideomotor perspective (e.g., Greenwald, 1970; Prinz, 1987), ideomotor representations and simple S-R associations have different underlying learning mechanisms. Ideomotor representations originate from learning the relationship between actions and subsequent sensory effects (R-E learning). This form of learning is available whenever, for example, we perform an action with our hand and we see our hand moving and is normally implicit. Throughout this visuo-motor experience, the system becomes able to predict the sensory consequences of motor commands (e.g., Hommel, 2009). In contrast, classical associative learning theories primarily focus on learning the relationship of responses to those stimuli that precede them

(S-R learning). Most experiments which demonstrates that imitative response tendencies can easily be suppressed, use paradigms where participants are explicitly instructed to translate observed stimuli in performance (S-R associations) rather than R-E learning paradigms (e.g., Catmur et al. 2007). Both implicit and explicit processes are certainly critical for learning. Different kinds of sensorimotor experience is received during development, whenever infants watch their hands moving, engage in synchronous action with others, or deliberately imitate adults to learn how to do something (Heyes, 2001). However, implicit motor-to-vision forms of learning are likely to occur prior to the explicit vision-to-motor form.

Our results may also contribute to the debate concerning complementary actions. Previous studies showed that response tendencies can rapidly switch from imitative to complementary action according to task demands (Newman-Norlund et al., 2007; van Schie et al., 2008). Recent neuro-imaging evidence suggests that this rapid task-dependent reorganization may require two sets of brain areas: regions within the mirror system, which translates motor and visual codes, and prefrontal, posterior parietal, and temporal areas adjacent to mirror system, which integrates the information to achieve common goals (Kokal et al., 2009). Our results support the idea that response flexibility can recruit mechanisms outside the mirror system and interact with other perceptuomotor systems. In effect, it is very unlikely that verbal instructions alone could have modified the mirror system.

Cognitive and motor flexibility are fundamental abilities for our survival along the life span and the mirror system must submit to this rule. Here we have unraveled one of the crucial mechanisms that might allow for such flexible adjustments. Nonetheless, future research is needed to better qualify the effect of task instructions on the mirror system both in terms of cognitive and neural processes.

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