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Sensorimotor Training Alters Action Understanding

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Abstract

The discovery of 'mirror' neurons stimulated intense interest in the role of motor processes in social interaction. A popular assumption is that observation-related motor activation, exemplified by mirror neurons' matching properties, evolved to subserve the 'understanding' of others' actions. Alternatively, such motor activation may result from sensorimotor learning. Sensorimotor training alters observation-related motor activation, but studies demonstrating training-dependent changes in motor activation have not addressed the functional role of such activation. We therefore tested whether sensorimotor learning alters action understanding. Participants completed an action understanding task, judging the weight of boxes lifted by another person, before and after 'counter-mirror' sensorimotor training. During this training they lifted heavy boxes while observing light boxes being lifted, and vice-versa. Compared to a control group, this training significantly reduced participants' action understanding ability. Performance on a duration judgement task was unaffected by training. These data suggest the ability to understand others' actions results from sensorimotor learning.

Keywords: social cognition, motor system, mirror neuron, action understanding, sensorimotor learning

1. Introduction

Whether, and to what extent, the motor system plays a role in the perception and understanding of observed actions is a matter of fierce debate within cognitive science. There is relatively unambiguous evidence that motor-related neural structures are activated by action observation, exemplified by over two decades of research on mirror neurons (motor-related neurons which fire during both action performance and observation of another performing a related action; di Pellegrino et al., 1992); but the function of such observation-related motor activation is still unclear. Some theorists argue that motor activation plays a causal role in the perception and understanding of others' actions ('embodied simulation'; Gallese & Sinigaglia, 2011), whereas others argue that motor activation is the consequence (not cause) of action perception and understanding (Mahon & Caramazza, 2008), or that motor activation contributes to action perception in a domain-general fashion, impacting on processes such as attention and rhythm perception that are recruited for action and non-action stimuli alike (Press & Cook, 2015).

Questions concerning the function of observation-related motor activation are orthogonal to questions concerning the origin of such activation, but empirical evidence pertaining to one question has often been used to support a position with respect to the other. For example, supporters of embodied simulation theories argue that mirror neurons within the motor system subserve the 'understanding' of others' actions (Rizzolatti et al., 1996); and that the matching properties of mirror neurons evolved specifically to subserve such 'action understanding' (Fogassi, 2014; Gallese et al., 2009).

An alternative to such theories is that observation-related motor activation originates from sensorimotor learning in which the perceptual representation of an action is associated with the motor program for that action (Cook et al., 2014). This theory is well supported by empirical data; for example, 'counter-mirror' sensorimotor training (associative training in which observation of one action is systematically paired with performance of another action, for example performing an index finger action while observing a little finger action) has reliably been shown to change mirror neuron responses (Catmur et al., 2007; Cavallo et al., 2014; de Klerk et al., 2015; Petroni et al., 2010; Press et al., 2012).

However, the question of whether sensorimotor learning alters not only observation-related motor activation, but also the 'understanding' of others' actions, has not been addressed (Rizzolatti & Sinigaglia, 2010; see also Hickok, 2009). In particular, supporters of the embodied simulation account have proposed that although sensorimotor training may alter observation-related motor activation, it would not affect action understanding because 'movement mirroring' is distinct from 'goal mirroring' (Rizzolatti & Sinigaglia, 2010, p. 269). In contrast, the sensorimotor learning account predicts that any learning that alters observation-related motor activation should also alter action understanding, if action understanding relies on such activation. The present study therefore addressed this gap in the literature by testing whether sensorimotor learning, the process theorized to give rise to observation-related motor activation, alters the hypothesized function of such activation, action understanding.

The term 'action understanding' has been used to refer to various stages in processing others' actions, including: action perception (Pobric & Hamilton, 2006; Saygin et al., 2004); identification of the 'goal' of an action (Rizzolatti & Fabbri-Destro, 2008); and identification of the actor's underlying intentions (Iacoboni et al., 2005). As we have recently argued (Catmur, 2014, 2015), there is little empirical evidence supporting the involvement of motor processes in identifying intentions from actions; but there is some evidence that motor brain areas, including areas thought to contain mirror neurons, are involved in aspects of action perception, including the ability to discriminate between actions based on perceptual differences. The clearest demonstration of the role of motor areas in action perception utilizes a task (Runeson & Frykholm, 1981) in which participants judge a box's weight by watching videos of a hand lifting the box and placing it on a shelf. Performance on this task is disrupted by repetitive transcranial magnetic stimulation to inferior frontal gyrus (Pobric & Hamilton, 2006), consistent with the idea that motor-related areas are required to perform this task (see also Moro et al., 2008; Saygin, 2007; Hayes et al., 2007).

In the present study, we therefore use 'action understanding' to refer to perceptual discrimination between actions, as the definition where there is most evidence of a motor (and possibly therefore mirror neuron) contribution. Thus the fairest test of whether sensorimotor learning affects action understanding as well as producing observation-related motor activation is to use the definition of action understanding for which a motor contribution has been demonstrated.

Participants in the present study therefore completed an action understanding task in which they judged the weight of boxes lifted by another person, before and after 'counter-mirror' sensorimotor training. During this training, they lifted heavy boxes while observing light boxes being lifted, and vice-versa. The control group received 'mirror' sensorimotor training, wherein they lifted heavy boxes while observing heavy boxes being lifted, and lifted light boxes while observing light boxes being lifted. As both groups received equal motor and visual experience, any differential effects of training must be due to the type of sensorimotor experience received.

Participants also completed a control, duration judgement, task before and after training, to verify that any effects of sensorimotor training were specific to the weight judgement task. If sensorimotor learning alters action understanding then training type (counter-mirror versus mirror) should affect performance on the weight judgement task, but not on the duration judgement task.

2. Method

2.1. Participants

Fifty-six participants (16 male, ten left-handed) aged 17-53 years (mean 20.6, standard deviation (SD) 5.1) were recruited via the University of Surrey and King's College London experiment participation pools and randomly allocated to the mirror or counter-mirror training group. Two participants were replacements for participants who failed to follow task instructions (by using a very truncated scale for the duration judgement task). Participants received course credit or remuneration for their time. Experimental procedures were approved by the local Ethics Committees and followed the Declaration of Helsinki.

2.2. Stimuli and Materials

Stimuli for the weight judgement task were taken from Pobric and Hamilton (2006) and comprised five videos of a hand lifting visually indistinguishable boxes of five different weights (approximately 50g, 250g, 450g, 650g, and 850g). Each video (4400ms duration) commenced with an image of a box on a table next to a low shelf. After a short delay a hand entered the screen from the right, lifted the box, placed it on the shelf, and exited the screen (see Figure 1).

Figure 1. Screenshots from an exemplar box lifting video.

Stimuli for the duration judgement task were based on the 450g weight video, which was edited by removing or adding frames to the action part of the video such that the hand was visible for five different durations (83, 88, 93, 98, and 103 frames; videos were presented at 25 frames per second). Two additional videos were constructed, in which the hand was visible for 90 and 96 frames, for use in initial familiarization. These durations did not correspond to any presented in the main experiment.

Four visually indistinguishable boxes were constructed, made of black plastic and measuring 85x56x39mm, with lead weights inside. Two boxes weighing 350g and 550g were used in initial familiarization. These weights did not correspond to any presented in the main experiment. The other two boxes (50g and 850g) corresponded to the weights of the boxes in the lightest and heaviest videos of the weight judgement task, and were used in the training session.

2.3. Procedure

Participants were tested in three sessions. During the first (test) session they completed the weight and duration judgement tasks (order was counterbalanced across participants). During the second (training) session they received either mirror or counter-mirror sensorimotor training. The third (test) session was identical to the first. The second and third sessions took place on consecutive days. The mean delay between the first and second sessions was 9 days (SD 14.4) and did not differ across training groups (*p*=.36).

The weight judgement task was based on Pobric and Hamilton (2006) and Hamilton et al. (2007). On each trial, participants were presented with one of the five weight judgement videos and judged the weight of the box using a scale of 0-90[1]. Each trial commenced with a fixation cross (duration assigned at random from 800, 1000, 1200 and 1400ms), followed by presentation of the video. After the video, a question screen (‘how heavy was the box?’) was presented until the participant responded by entering the weight using the numeric keypad and pressing Enter to move on to the next trial. Eighty trials (16 per weight video) were presented in random order in two blocks of 40 trials. Five practice trials (one per weight

[1] Hamilton et al. (2007) used a 0-100 scale but given the veridical weights of the boxes the use of 100 as the upper anchor introduced a non-linearity into their scale; an upper anchor of 90 ensures a linear scale for the weights used.

video) were presented before the first block and were not analyzed. Stimuli were presented and responses recorded using E-Prime2 (Psychology Software Tools, Sharpsburg, PA) running on a Dell Optiplex 9030 with a 23" LCD monitor (resolution 1920x1080, refresh rate 59Hz).

The duration judgement task was identical to the weight judgement task with the exceptions that the five duration judgement videos were presented, and the question asked 'how long was the hand visible?'

Before the main tasks, participants were given instructions and a familiarization procedure. Participants were told: they would see videos of a hand lifting a box and placing it on a shelf; the videos would vary in terms of either the weight of the box or the duration that the hand was visible; in both cases these values would range between 0 and 90; and that their task was to report how heavy the box was or how long the hand was visible, using the full range of the 0-90 scale. It was explained that the 0-90 scales were in arbitrary units, and to help participants appreciate the range of the scales, they would be familiarized with two points within each scale for both weight and duration judgement tasks. Participants were given each of the two familiarization weights to hold, and were told that these equated to weights of 35 and 55 units on the 0-90 scale. They also watched the two familiarization duration videos, and were told that the hand was visible for durations of 35 and 55 units on the 0-90 scale.

During sensorimotor training, a screen was positioned in front of participants such that they could see the monitor (at eye level) but nothing below eye level. Their right hand was placed on a table behind the screen and a low shelf was on the table to their left. On each trial, a cue was presented to the experimenter (occluded from the participant's view), instructing whether the light (50g) or heavy (850g) training box should be used on this trial. The experimenter then slid the appropriate box into position next to the participant's hand,

and initiated video playback. The participant was instructed to reach, grasp, lift and place the box on the shelf in synchrony with the action in the video (confirmed by the experimenter on every trial), without seeing their own hand. After the video, a fixation cross was presented until the experimenter initiated the next trial. Each trial lasted approximately 11 seconds. Training comprised six training blocks of 40 trials per block, on half of which the video was the lightest weight (50g), and on half of which it was the heaviest weight (850g). Participants in the mirror training group lifted a light box when a light box video was presented, and a heavy box during a heavy box video; whereas participants in the counter-mirror training group lifted a light box when a heavy box video was presented, and a heavy box during a light box video.

3. Results

Responses over 90, and trials on which participants made no response, were excluded. For every participant, task, and session, the mean and SD response for each video was then calculated, and outlying responses >2SD from the mean were excluded. Figure 2 displays the mean responses for each training group, task, and session.

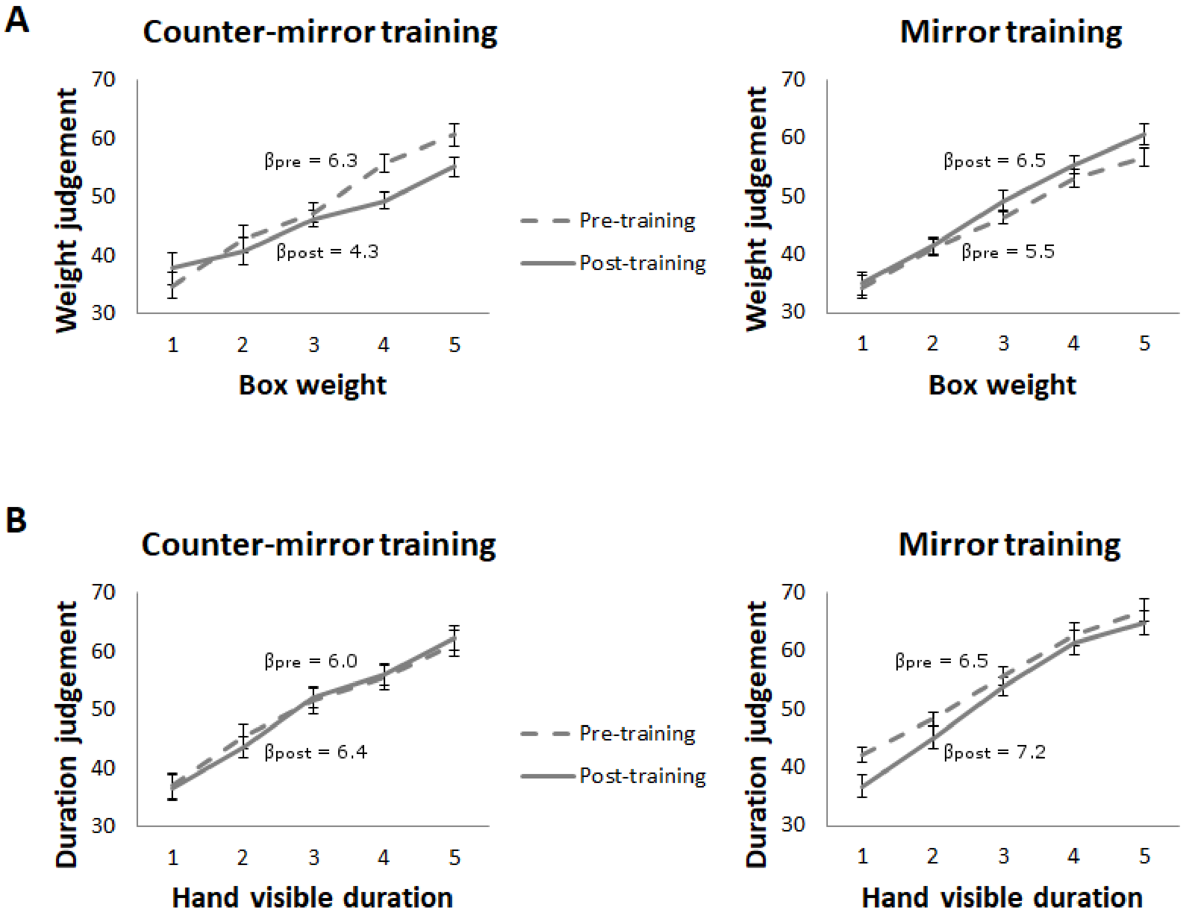

Figure 2. Mean ± standard error of the mean performance on A. the weight judgement and B. the duration judgement tasks in the two training groups before and after training. β values indicate the regression line slope. Counter-mirror training reduced performance on the weight judgement task, whereas performance on the duration judgement task was unaffected by training.

Performance was assessed by regressing participants' judgements for each video onto the actual weight or duration of that video (as in Runeson & Frykholm, 1981; Pobric & Hamilton, 2006; Hamilton et al., 2007). This produced a regression line with values for slope (β indicating accuracy) and goodness-of-fit (r; indicating variability) for every participant for each task and each session. Figure 3 displays the data and regression line from a representative participant for the weight judgement task.

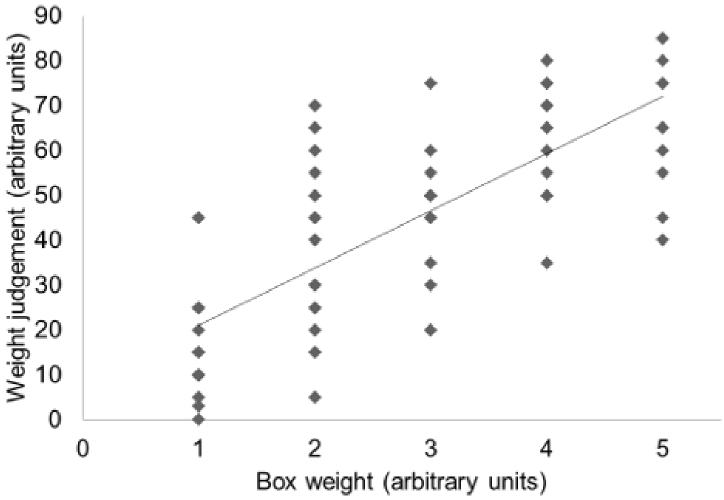

Figure 3. Performance of a representative participant on the weight judgement task.

The slopes for the weight judgement task were subjected to Analysis of Variance (ANOVA) with between-subjects factor of training group (mirror, counter-mirror) and within-subjects factor of session (pre-training, post-training). Neither of the main effects reached significance, however a significant interaction was found, $F(1,54)=11.04$, $p=.002$, $\eta^2_p=.170$. As indicated in Figure 2, regression slopes were less steep for the counter-mirror training group in the post-training session, indicating worse ability to use the videos to judge box weight after counter-mirror sensorimotor training. Analysis of the simple effect of session confirmed a significant difference between regression slopes in the two sessions in the counter-mirror training group, $F(1,54)=10.50$, $p=.002$, $\eta^2_p=.163$. This was not present in the mirror training group. Furthermore, regression slopes in the counter-mirror and mirror training groups were significantly different in the post-training session, $F(1,54)=4.68$, $p=.035$, $\eta^2_p=.080$, but not in the pre-training session.

Regression slopes for the duration judgement task were subjected to the same ANOVA and revealed no significant effects, crucially demonstrating no interaction between training group and session, $F(1,54)=0.16$, $p=.687$, $\eta^2_p=.003$.

Confirmatory analyses in which the units of analysis were: regression slopes standardized to the range of values used by each participant in the pre-training session (in order to control for possible individual differences in the use of the full range of values); tests for linearity of regression slope across the five videos; and correlation coefficients describing the goodness-of-fit of the data to the regression slope, all produced the same pattern of significance (see Table 1).

	Weight judgement task					**Duration judgement task**		
	Main effects		Interaction group x session	Simple effects		Main effects		Interaction group x session
Unit of analysis	Group	Session		Session in counter-mirror group	Group in post-training session	Group	Session	
Standardized regression slope	n.s.	n.s.	$F_{1,54}$ = 9.263 *p* = .004 η^2_p = .146	$F_{1,54}$ = 8.068 *p* = .006 η^2_p = .130	$F_{1,54}$ = 5.016 *p* = .029 η^2_p = .085	n.s.	n.s.	n.s.
Test of linearity across the five videos	n.s.	n.s.	$F_{1,54}$ = 10.346 *p* = .002 η^2_p = .161	$F_{1,28}$ = 7.247 *p* = .012 η^2_p = .206	$F_{1,54}$ = 4.220 *p* = .045 η^2_p = .072	n.s.	n.s.	n.s.
Goodness of fit	n.s.	n.s.	$F_{1,54}$ = 7.998 *p* = .007 η^2_p = .129	$F_{1,54}$ = 5.296 *p* = .025 η^2_p = .089	$F_{1,54}$ = 6.073 *p* = .017 η^2_p = .101	n.s.	$F_{1,54}$ = 4.087 *p* = .048 η^2_p = .070	n.s.

Table 1. Confirmatory analyses demonstrating the same patterns of significance for the weight judgement task across all units of analysis.

4. Discussion

The present study built on previous evidence that sensorimotor learning may underpin observation-related motor activation. It investigated whether sensorimotor learning impacts what has been claimed to be the primary function of such activation: action understanding. Counter-mirror sensorimotor training significantly reduced action understanding performance, indexed by the weight judgement task; and this training was selective: the control task was unaffected by training. Participants in the mirror training group received equal visual and motor experience of box lifting, indicating that sensorimotor learning, rather than visual or motor learning (Calvo-Merino et al., 2006; Cross et al., 2009), produced the changes in action understanding. These results suggest that sensorimotor learning influences action understanding, supporting the proposal that the ability to understand others' actions may result from sensorimotor learning.

One possible objection to our conclusion is that participants could have extracted an explicit rule from the training session (e.g. 'the boxes that look heavy are light'). We consider this unlikely since when we explained the training manipulation to participants at debrief, they were unsure as to which training group they were in, suggesting they had not explicitly encoded the relationship between the weights of the boxes in the videos and those which they lifted.

These data build on previous work (e.g. Hamilton et al., 2004) providing evidence for the role of motor processes in action understanding, and – to the extent that links between observed and executed actions are mediated by mirror neurons – evidence for a role of mirror neurons in action understanding. Furthermore, they suggest that the process which produces mirror neurons' matching properties (Cook et al., 2014) may provide them with one of their primary functional attributes. These results may be considered consistent with an account of mirror neuron development in which neurons have initial mirror properties that are refined through learning (Gallese et al., 2009; Casile et al., 2011). However, a central property of accounts which posit that the properties of a system are a functional adaptation to improve evolutionary fitness (Rizzolatti & Craighero, 2004; Fogassi, 2014; Oberman et al., 2014) is that those properties should be buffered against perturbation by the type of experience present in the environment in which those properties evolved (Cosmides & Tooby, 1994; Pinker, 1997). The finding, therefore, that a relatively short period of sensorimotor learning is sufficient to disrupt the functional properties of the system (making participants worse at action understanding) is not consistent with those properties being an adaptation that evolved to fulfil that particular function.

These data illustrate that action understanding may depend on experience, and thus emphasize the importance of the early sociocultural environment for development of behaviors crucial to social interaction, including the ability to understand others' actions (Heyes, 2012; Cook et al., 2013). They also suggest that interventions utilizing sensorimotor training may help improve social interaction.

In conclusion, we demonstrate that a common process of sensorimotor learning may underpin the development of both the observation-related motor activation exemplified by mirror neurons' matching properties, and the functional role of such motor activation.

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