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Citation: Roberts, James W., Constable, Merryn, Burgess, Raquel, Lyons, James L. and Welsh, Timothy N. (2018) The influence of intrapersonal sensorimotor experiences on the corticospinal responses during action-observation. *Social Neuroscience*, 13 (2). pp. 246-256. ISSN 1747-0919

Published by: Taylor & Francis

URL: <https://doi.org/10.1080/17470919.2017.1289979>
<<https://doi.org/10.1080/17470919.2017.1289979>>

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**The influence of intrapersonal sensorimotor experiences on the corticospinal responses
during action-observation**

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Acknowledgement This work was supported by the Natural Sciences and Engineering
Research Council of Canada; under Grant [number 386762-2010 RGPIN] and under Grant
[number 2015-06482].

[This is an Accepted Manuscript of an article published by Taylor & Francis in Social Neuroscience on 24/01/2017, available online:

<http://www.tandfonline.com/10.1080/17470919.2017.1289979>]

Abstract

The coupling of perception and action has been strongly indicated by evidence that the observation of an action primes a response in the observer. It has been proposed that these primed responses may be inhibited when the observer is able to more closely distinguish between self- and other-generated actions – the greater the distinction, then the greater the inhibition of the primed response. This self-other distinction is shown to be enhanced following a period of visual feedback of self-generated action. The present study was designed to examine how sensorimotor experiences pertaining to self-generated action affect primed responses from observed actions. Single-pulse transcranial magnetic stimulation was used to investigate corticospinal activity elicited during the observation of index- and little-finger actions before and after training (self-generated action). For sensorimotor training, participants executed finger movements with or without visual feedback of their own movement. Results showed that the increases in muscle-specific corticospinal activity elicited from action-observation persisted after training without visual feedback, but did not emerge following training with visual feedback. This inhibition in corticospinal activity during action-observation following training with vision could have resulted from the refining of internal models of self-generated action, which then led to a greater distinction between ‘self’ and ‘other’ actions.

Keywords:

Action-observation, Perception-action coupling, Inhibition, Sensorimotor experience, Corticospinal excitability

Introduction

It is understood that there is a coupling between the neural codes representing the perceptual effects of an action and the neural codes that lead to the execution of an action; a process referred to as *perception-action coupling*. As a consequence of this coupling, it is suggested that the observation of another person's action maps onto and activates a corresponding motor representation within the observer (Hommel, Müssele, Aschersleben, & Prinz, 2001; Oberman & Ramachandran, 2007; Prinz, 1997; Rizzolatti & Singaglia, 2010). Behavioural evidence supporting the activation of the corresponding motor representation comes from a series of reports that responses take longer to initiate (Brass, Bekkering, & Prinz, 2001; Brass, Bekkering, Wohlschläger, & Prinz, 2000) or are executed with greater error (Kilner, Paulignan, & Blakemore, 2003; cf. Constable, de Grosbois, Lung, Tremblay, Pratt & Welsh, in press) when the observed response of another person is incongruent with the action the observer is executing (e.g., observing a vertical arm movement while simultaneously executing a horizontal arm movement). It is suggested that these interference effects emerge because the observation of an incongruent action elicits a corresponding motor representation of the incongruent action within the observer, and then interferes with the coding and the generation of the intended or instructed action (Blakemore & Frith, 2005).

Many researchers have proposed that these interference effects result from an action-observation or mirror-matching system within the human brain (Iacoboni & Dapretto, 2006; Rizzolatti & Craighero et al., 2004). Neuro-imaging data has extensively supported this claim by showing that there is an overlap of neural regions (including the inferior parietal lobule [IPL], inferior frontal gyrus [IFG] and/or ventral premotor cortex [vPM]) that are activated by both the observation and execution of a single action (Cross, Kraemer, Hamilton, Kelley, & Grafton, 2009; Gazzola, Rizzolatti, Wicker, & Keysers, 2007; Iacoboni et al., 1999). More direct neurophysiological evidence for the activation of motor representations during action-

observation has been derived from studies using single-pulse transcranial magnetic stimulation (TMS). Indeed, when single-pulse TMS is delivered over the primary motor cortex (M1) during action-observation, there is an increase in the amplitude of motor-evoked potentials (MEPs) at the precise musculature (e.g., first dorsal interosseous [FDI]) featured within the observed action (e.g., index finger abduction/precision grip) (Alaerts, Swinnen, & Wenderoth, 2009; Cattaneo, Caruana, Jezzini, & Rizzolatti, 2009; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Gangitano, Mottaghy, & Pascual-Leone, 2001; Sartori, Xompero, Buccioni, & Castiello 2012). The increase in MEP amplitude is thought to occur because of increases in the excitability of the cortical neurons representing the observed action within the observer. That is, the observation of an action activates the same neurons as when the observer actually executes the action.

Recently, there has been evidence that factors such as social context can modulate the magnitude of responses derived from perception-action coupling during action-observation. For example, the initial priming of a pro-social or anti-social attitude can subsequently modulate motor interference (e.g., Cook & Bird, 2011; Leighton, Bird, Orsini, & Heyes, 2010; Roberts, Bennett, & Hayes, 2015) as well as corticospinal excitability during action-observation (Hogeveen & Obhi, 2012; Obhi, Hogeveen, & Pascual-Leone, 2011). This modulation has been attributed to the regions of the brain typically associated with social cognition including the medial prefrontal cortex (mPFC) and right temporo-parietal junction (rTPJ) (Brass, Ruby, & Spengler, 2009; Santiesteban, Banissy, Catmur, & Bird, 2012; Sowden & Catmur, 2015). Interestingly, these neural regions are also implicated in distinguishing between self- and other-generated actions. Due to this functional overlap, it is reasonable to predict that the modulation of perception-action coupling is inversely related to the distinction between self and others (see Sowden & Shah, 2014, for a review). That is, by

decreasing (or increasing) the distinction between self and other there may be an increase (or decrease) in the magnitude of primed responses following action-observation.

In addition to these high-level socio-cognitive processes, there may be low-level processes that also contribute toward the distinction between self and other. To elucidate, self-generated actions entail the generation of a forward model that enables the prediction of the upcoming 'state' of the system along with its sensory consequences (Wolpert & Ghahramani, 2000; see also von Holst, 1954). Whenever the anticipated and actual sensory consequences are closely matched, then they are assumed to be a product of the 'self' (Blakemore, Wolpert, & Frith, 2000; Shergill, Bays, Frith, & Wolpert, 2003; Shergill, Samson, Bays, Frith, & Wolpert, 2005). Alternatively, when the anticipated and actual sensory consequences are mismatched, then they are attributed to 'other' sources. It is through this process that we may garner a 'sense of agency', as reflected by the 'intentional binding' effect (Haggard, Clark, & Kalogeras, 2002). The intentional binding effect refers to how the perceived time of an external sensory event (i.e., auditory tone) and the preceding voluntary action (i.e., executed finger press) can become more closely bound together compared to the same sensory event taking place after an involuntary movement (i.e., a movement generated via cortical TMS). Therefore, in the context of a forward model, it appears the generation of a forward model elicits predicted sensory consequences, which can then bias or attenuate the judgement of the actual sensory events and become coupled with the executed action.

Of interest to the present study, it has been shown that a period of stimulus-response associative learning can enhance the intentional binding effect (Moore, Dickinson, & Fletcher, 2011; Moore, Wegner, & Haggard, 2009). In other words, an increase in an individual's sensorimotor experience gained through training enhances intentional binding. This enhancement may unfold because the repeated and consistent pairing of an executed

action and given sensory event leads to an association in which the external sensory feedback is coupled or integrated with the internal model of action (Hayes, Andrew, Elliott, Roberts, & Bennett, 2012a; Wolpert & Flanagan, 2010; Wolpert & Ghahramani, 2000; see also Elsner & Hommel, 2001). This integration may be able to accommodate and enhance the distinction between self and other, which may enable the observer to inhibit primed responses and/or isolate the response codes that are typically evoked during action-observation. Therefore, the primed responses elicited by action-observation should decrease following relevant sensorimotor experiences.

Although the prediction that observation-evoked responses decreasing following sensorimotor experiences may seem logical, recent studies have focused on the influence of prior sensorimotor experiences on response priming to elucidate the mechanisms that mediate perception-action coupling. That is, the investigations of imitation and mimicry have led to the conclusion that enhancing stimulus-response associations formed throughout the lifespan can enhance the imitation or mimicry of observed actions (e.g., Cook, Dickinson, & Heyes, 2012; Cook, Press, Dickinson, & Heyes, 2010; Heyes, Bird, Johnson, & Haggard, 2005; Press, Gillmeister, & Heyes, 2007). In support of this view, it is shown that the imitation effects generated by the observation of congruent compared to incongruent actions can be attenuated or reversed after an extended period of incompatible stimulus-response training. That is, the shorter response times for closing the hand when observing a hand closing compared to observing a hand opening became attenuated and reversed after observers completed a training phase in which they paired their response with the incongruent stimulus (e.g., closing their hand while observing a hand open). In addition, the increased corticospinal activity that is shown during action-observation can be relocated to the precise musculature adopted during incompatible stimulus-response training (Catmur, Walsh, & Heyes, 2007; see also complementary/reciprocal responses; Sartori, Bucchioni, & Castiello, 2013). For

example, Catmur et al. (2007) reported that, following a series of training trials in which the execution of *index* finger abduction coincided with the observation of a model abducting the *little* finger, the peak-to-peak amplitude of MEPs generated in the FDI (index finger abductor) began to increase during the observation of the incongruent little finger abduction. These works have heavily substantiated the Associative Sequence Learning theory, which suggests that the perception-action coupling underlying imitation is subject to factors of ontogeny (i.e., environment-based) rather than phylogeny (i.e., evolution-based) (Heyes, 2001; Heyes & Ray, 2000).

However, it is interesting to note that these sensorimotor experiences are suggested to entail both interpersonal and intrapersonal encounters (Heyes, 2010). That is, the stimulus-response associations may be equally formed by responses to the observed actions of others or by observing our very own actions, respectively. The research thus far on sensorimotor experiences modulating observation-evoked response activation has focused on *interpersonal* sensorimotor experiences. However, the aforementioned efferent and reafferent processes associated with self-generated action (Blakemore et al., 2000) and the potential overlap between self-other distinction and response modulation (Brass et al., 2009) may predict an alternative outcome from *intrapersonal* sensorimotor experience. Indeed, it could be predicted that the stimulus-response associations formed from self-generated actions may encompass a sensorimotor representation that refines one's sense of agency, and thus works to isolate and inhibit primed responses during the observation of another person's actions.

The following study was designed and conducted to investigate the influence of intrapersonal sensorimotor experiences on the corticospinal activity elicited by observed actions. To this end, single-pulse TMS was applied to M1 to evoke MEPs from FDI and ADM during the observation of an index and little finger abduction movement at baseline and post-training test phases. Participants completed the assessment of observation-induced

corticospinal excitability at baseline and after gaining sensorimotor experience (training) of index and little finger abduction movements. Both the test phase observations and related sensorimotor experiences featured two separate effectors in order to fulfil our further aim of determining whether sensory-specific visual feedback is relevant to the influence of training on the modulation of corticospinal excitability. As a result, each participant completed two separate training phases featuring different visual feedback conditions - in one condition, the finger movement (e.g., index finger abduction) was trained with visual feedback of the moving finger, while in the other condition the alternative finger movement (e.g., little finger abduction) was trained without visual feedback (i.e., occlusion).

Based on previous research (e.g., Fadiga et al., 1995), it was expected that there would be an increase in corticospinal activity following action-observation on congruent trials (e.g., MEPs from FDI while observing index finger abduction) compared to incongruent trials (e.g., MEPs from FDI while observing little finger abduction) during the baseline pre-training assessment. If intrapersonal sensorimotor experiences mediating the distinction between self- and other-generated actions fail to modulate primed responses (as indexed by increased corticospinal activity during the observation of congruent compared to incongruent actions), then we would expect the enhanced baseline activity found in congruent compared to incongruent trials to persist at the post-training phase. On the other hand, if intrapersonal sensorimotor experiences mediating the distinction between self and other begin to modulate primed responses, then we would expect the enhanced baseline activity found in congruent compared to incongruent trials to dissipate at the post-training phase. Moreover, if these sensorimotor experiences are contingent upon sensory-specific visual feedback, where external afferent information can become integrated with the efferent and reafferent sources of information, then we would expect the modulation of observation-evoked excitability to unfold only for the vision condition.

Method

Participants

Nineteen participants took part in the study (age range between 19 and 30 years) (one participant was excluded due to technical error leaving eighteen participants for analysis). All participants were self-reported right-handed, had normal or corrected-to-normal vision and no neurological disorders. None of the participants had any contraindications to TMS. The experiment was approved by the University of Toronto ethics committee and conducted in accordance with the 1964 Declaration of Helsinki.

Stimuli and Procedure

Stimuli were displayed on a LCD computer monitor that was placed 50 cm from the participant with a temporal resolution of 60 Hz and spatial resolution of 1024 x 768 pixels. The stimulus was presented via a custom-written script in MATLAB (The Mathworks Inc.), using Cogent 2000 toolbox. The stimulus featured an image of a hand at rest taken from the dorsal view in the first-person perspective. Following a variable interval (800-2400 ms), the stimulus hand would remain at rest or switch to a posture with the index or little finger being abducted. The sudden change in image from rest to abduction of the index or little finger gave rise to apparent motion of the finger (see Catmur & Heyes, 2011 and Press et al., 2007 for examples).

The experiment was completed in a single session that took approximately 1.5 hrs to complete. The procedure comprised a test-retest protocol featuring two types of training interventions (Figure 1). In the baseline and post-training tests of corticospinal excitability, participants were instructed to closely observe the hand stimulus presented on a screen and to press the X-key of the keyboard with the left hand in the event a white dot (20 mm-diameter) appeared on the stimulus hand. The appearance of the dot unfolded in pseudorandom fashion

with an equal number of occurrences for each of the different types of stimuli (static hand, index finger, little finger). This task was developed to ensure that participants paid close attention to the hand stimulus even though the finger movement was irrelevant to the task from the participants' perspective (see Catmur et al., 2007). There were a total of 63 trials in the baseline and post-training phases which consisted of 21 trials for each stimulus condition (little finger abduction, index finger abduction, and rest). There were only 6 trials in which the white dot appeared. All participants provided 100% correct responses for the detection of the white dot indicating that they closely watched the hand stimuli. The type of finger movement was presented at random with the caveat that no one stimulus condition could be presented more than twice in a row.

In between the baseline and post-training phases, participants undertook the sensorimotor training phase in which they completed a series of abduction movements with the index or the little finger. Participants only moved one of the fingers during a given set of training trials. Participants were instructed to repeatedly abduct the index or little finger at a rate of 1 Hz for up to 3 minutes (i.e., 180 movements). The rate of execution was initially guided by an auditory metronome (1 Hz) for the first 30 seconds of the movement (i.e., 30 movements). The metronome was then turned off so that the participant continued the movement unaided. Two experimenters were present and monitored the movement training protocol to ensure the participant successfully upheld the movement criterion. The experimenters used a stopwatch to ensure the pacing and length of movement was consistent with the instructions. If a participant was unable to execute the movement in-time with the metronome during the initial 30 seconds, then they were instructed to re-start the training procedure. However, there were no instances in which either of the experimenters reported such difficulty in this relatively simple motor task.

For the training phase of the no vision condition protocol, participants wore a blindfold so they could not see the movements of their own finger. For the training phase of the vision condition protocol, no blindfold was worn and participants were instructed to closely observe their moving finger. The order of the vision conditions (i.e., vision/ no vision) and the assignment of the finger for each visual condition (i.e., index/little finger movements) were counter-balanced between participants. In other words, one half of the participants received visual feedback when training with the index finger, and no visual feedback when training with the little finger, while the other half received visual feedback when training with the little finger, and no visual feedback when training with the index finger.¹

[Insert Figure 1 about here]

TMS and MEP recordings

MEPs were detected by two disposable 3M red dot model 2560 Ag/AgAl surface electrodes that assumed the belly-to-belly montage over the first dorsal interosseous (FDI) and abductor digiti minimi (ADM). The two electrodes were placed over the longitudinal axis of the muscle between the motor point/innervation zone (i.e., distal location where the muscle becomes innervated at the muscle endplate) and the tendinous insertion (Stegeman & Hermens, 2007). The adhesive pads securing the surface electrodes were cut to size in order to uphold the correct positioning and obtain an inter-electrode distance of ~1 cm. The third (ground) electrode was placed directly over the lateral epicondyle of the elbow. EMG data were recorded and processed through Brainsight software (Rogue Research, Montreal, QC). Signals were sampled at 3000 Hz and band-pass filtered between 16 Hz and 470 Hz. The recording interval was time-locked to 50 ms prior to stimulation and ended 150 ms after the stimulation (see White, Reid, & Welsh, 2014).

TMS was delivered by the MagStim 200 (The MagStim Company, Carmanthenshire, UK) using a 70 mm figure-of-eight coil (70 mm). The coil was placed over the left primary motor cortex (M1) that was initially positioned at an angle subtending 45° from the interhemispheric fissure and perpendicular to the central sulcus. A conventional mapping and resting motor threshold procedure was employed. That is, the optimal scalp position was defined as the site that consistently produced the largest MEPs in both the FDI and ADM. To find this area, a location 6 cm lateral and 2 cm anterior from the vertex was first located. Initial TMS pulses at 30% of the stimulator output were delivered over this site. If no MEPs were detected from this initial stimulation, then the coil was moved in roughly 1 cm increments around this initial location. Each stimulus was delivered 4-8 seconds apart. If MEPs were still not observed after this incremental search, the coil was returned to the initial location and the search procedure was repeated with a 5% increase in stimulator output (i.e., taking the first iteration of the stimulator output to 35%). Once an MEP was observed, the location and orientation of the coil was adjusted around this location until the largest and most consistent MEPs were observed. This location and orientation was deemed the “motor hotspot”, and the coordinates and orientation of the coil of the hotspot were recorded in Brainsight to facilitate accurate re-placement of the coil. Although the MEPs elicited in FDI were generally of larger amplitude compared to the ADM, there were no cases in which the designated optimal site failed to feature both muscles being activated. Indeed, the FDI and ADM muscles assume satisfactorily similar areas (see Alaerts et al., 2009; Cavallo, Buccioni, Castello, & Becchio, 2013; Sartori, Buccioni, & Castello, 2012).

Once the optimal location was identified, the stimulator output was adjusted down and up in 1% increments until the resting motor threshold was identified. Resting motor threshold was determined as the stimulator output that resulted in a peak-to-peak MEP amplitude of at least 50µV for 5 out of 10 attempts in both the FDI and ADM, whilst the muscles were at

rest. Immediately prior to the testing phases, the coil was placed in the orientation and location recorded in Brainsight and a TMS pulse was delivered at resting motor threshold to ensure that an MEP could still be elicited. Providing the required peak-to-peak MEP amplitude was observed in both the FDI and ADM, the stimulator output was increased to the testing level (110% of the resting motor threshold) and the block of trials was initiated. Coil location and orientation (and hence the stimulated volume) were constantly monitored and adjusted during testing to ensure accurate and consistent location of stimulation. Test TMS stimuli were delivered at a variable interval (0 ms, 320 ms, 640 ms; see Catmur et al., 2007) following stimulus onset (the apparent abduction of the index or little finger). The desktop computer controlling the presentation of the stimuli also controlled the delivery of the 5V TTL signal (via a BNC connection) to the MagStim 200 to trigger the TMS pulse and EMG (Brainsight) system to commence recording of any muscle activity.

Data analysis

The EMG data from the pre-stimulation interval (-50 ms from TMS delivery) were analysed for any muscle pre-activation and background EMG. Specifically, trials that exceeded 3SDs of the within-participant root-mean-square error (RMSE) were excluded from the analysis.² The mean peak-to-peak MEP amplitude from the FDI and ADM muscles were assigned congruent and incongruent conditions with respect to the nature of the observed stimulus (i.e., index or little finger abduction). Thus, the MEP data for the FDI muscle was identified as congruent when the participant observed the index finger abduction, and was identified as incongruent when observing the little finger abduction. Conversely, the MEP data for ADM muscle was identified as congruent when the little finger abduction was observed and incongruent when the index finger abduction was observed. The participant means for congruent and incongruent conditions were normalized by dividing by the mean

for the control (i.e., hand at rest or static) condition. This procedure was designed to control for the between-participant and between-muscle variability in absolute MEP amplitude (see Catmur et al., 2007).

Trials on which the white-dot (i.e., attention check trials) did or did not appear were included in the analysis. Because the muscles of interest (FDI, ADM) were defined by their congruency with respect to the observed actions and the MEP amplitudes were normalized with respect to rest, the assignment of vision training protocols to particular individual effectors/muscles was not of theoretical relevance. Instead, the purpose of the fore mentioned procedure was to assess the overall impact of visual feedback in sensorimotor training on the corticospinal responses that are elicited during action-observation. Moreover, the corticospinal responses of interest are typically a function of the congruency shown between the effectors involved in the observed action (e.g., index finger) and area of excitation or measurement within the observer (e.g., FDI). Thus, the mean peak-to-peak MEP amplitudes were analysed using a repeated-measures ANOVA consisting of within-participant factors: phase (baseline, post-training), congruency (congruent, incongruent), and vision training (vision, no vision). Significance was declared at $p < 0.05$.

Results

There was no significant main effect of phase, $F(1, 18) = 0.23$, $MSE = 0.080$, $p = 0.64$, $partial \eta^2 = .01$, which would suggest there were no overall changes in peak-to-peak MEP amplitudes caused by time or TMS-exposure per se (see Sartori, Buccioni, & Castiello, 2012). There was a significant main effect of congruency, $F(1, 18) = 17.47$, $MSE = 0.010$, $p = 0.00$, $partial \eta^2 = .49$, indicating a higher peak-to-peak MEP amplitude for the congruent ($M = 1.02$, $SE = 0.02$) compared to the incongruent ($M = 0.98$, $SE = 0.03$) stimuli. There was no significant main effect of vision training, $F(1, 18) = 1.09$, $MSE = 0.054$, $p =$

0.31, $partial \eta^2 = .06$, nor interactions between phase and congruency, $F(1, 18) = 0.12$, $MSE = 0.027$, $p = 0.73$, $partial \eta^2 = .01$, phase and vision training, $F(1, 18) = 0.02$, $MSE = 0.036$, $p = 0.89$, $partial \eta^2 = .00$, and congruency and vision training, $F(1, 18) = 0.67$, $MSE = 0.045$, $p = 0.43$, $partial \eta^2 = .04$.

There was, however, a significant three-way interaction between phase, congruency and vision training, $F(1, 18) = 7.34$, $MSE = 0.045$, $p = 0.01$, $partial \eta^2 = .29$ (Figure 2). To understand the source of this interaction, two separate simple interaction effects (i.e., separate congruency by vision ANOVAs) for each level of phase (baseline, post-training) were conducted (Howell, 2013). For the analysis of the baseline data, there was no significant main effect of congruency, $F(1, 18) = 3.97$, $MSE = 0.027$, $p > 0.05$, $partial \eta^2 = .18$, nor vision training, $F(1, 18) = 0.65$, $MSE = 0.036$, $p > 0.05$, $partial \eta^2 = .03$. In addition, there was no significant interaction between congruency and vision training, $F(1, 18) = 2.05$, $MSE = 0.045$, $p > 0.05$, $partial \eta^2 = .10$. The analysis of the post-training data revealed no significant main effect of congruency, $F(1, 18) = 2.25$, $MSE = 0.027$, $p > 0.05$, $partial \eta^2 = .11$, nor vision training, $F(1, 18) = 1.00$, $MSE = 0.036$, $p > 0.05$, $partial \eta^2 = .05$. However, there was a significant interaction between congruency and vision training, $F(1, 18) = 5.76$, $MSE = 0.045$, $p < 0.05$, $partial \eta^2 = .24$. Simple main effect analysis on post-training data at each level of vision training (vision, no vision) revealed a significant congruency effect for no vision training, $F(1, 18) = 6.37$, $MSE = 0.045$, $p < 0.05$, $partial \eta^2 = .26$, but there was no significant effect of congruency for vision training, $F(1, 18) = 0.76$, $MSE = 0.045$, $p > 0.05$, $partial \eta^2 = .04$. These findings indicate that the increased corticospinal activity found for the observation of congruent compared to incongruent movements continued to emerge after training without visual feedback, but became attenuated following training with visual feedback.

[Insert Figure 2 about here]

Discussion

Observing another person's actions can involuntarily prime responses within the action-observation or mirror-matching system of the observer. This influence of action-observation is thought to occur because the observed action can map onto and activate the corresponding motor representation within the observer. The modulation of primed responses during action-observation may be mediated by a distinction between self- and other-generated actions with a limited primed response effect following an increased distinction. This distinction may result from the generation of a forward model of action and the related predicted sensory consequences of the person's own movement. These forward models can be refined and updated by sensorimotor experiences or stimulus-response associative learning. Thus, intrapersonal sensorimotor experience may decrease the priming of response codes following the observation of another person's movement because it accommodates a greater self-other distinction.

The current study tested this prediction by examining the influence of sensorimotor experiences pertaining to self-generated action on the corticospinal activity during action-observation. It was predicted that if intrapersonal sensorimotor experience enhances the distinction between self and other, then the increase in corticospinal activity that emerges during action-observation should be decreased following a period of intrapersonal sensorimotor training. Moreover, because the refinement and updating of internal models of action are contingent upon the integration of external sensory afference, it was predicted that this effect would unfold only for individuals that received visual feedback during training. On the other hand, training without visual feedback of the moving limb would not affect observation-induced corticospinal activity because the internal models would no longer be

refined and updated in the same way. The results confirmed that the increase in corticospinal activity following the observation of congruent compared to incongruent actions detected at baseline was no longer present after individuals were trained with visual feedback of their own movements. However, the increase in corticospinal excitability following action-observation continued to manifest following training without visual feedback.

To date, much of the research has adopted sensorimotor training in the context of enhancing perception-action coupling to indicate an increase in imitation (Heyes et al., 2005; Press et al., 2007), and corticospinal activity (Catmur et al., 2007). Indeed, the activation of the mirror-matching system (IPL, IFG, vPM) within the human brain appears to be larger following the observation of more familiar actions than less familiar actions (e.g., Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005; Cross, Hamilton, & Grafton, 2006). These works have been leveraged to formalise a theory of response-priming effects referred to as Associative Sequence Learning (ASL) theory, which states that sensorimotor experiences, including the observation and response to other-generated actions (interpersonal) and the observation of our own executed actions (intrapersonal), form an excitatory stimulus-response association that accommodates the imitation or mimicry of observed actions (Heyes, 2001; 2010). At first glance, the present findings may seem to conflict with the fore mentioned account because one might predict larger differences in congruent and incongruent action-observation following sensorimotor experience. However, the present data do in fact support the idea that the observation of actions forms a stimulus-response association. Nevertheless, in this instance, we suggest that intrapersonal sensorimotor experience results in changes to the forward model of self-generated action, which can then accommodate a distinction between self and other. This distinction can then contribute to the inhibition of observation-evoked primed responses (see later for further discussion). Notably, the difference between the present work and from the previous accounts comes from the nature

or source of sensory information because the sensorimotor experiences in our study pertain to an intrapersonal encounter (i.e., self-execution + self-observation) as opposed to training in an interpersonal setting (i.e., other-observation + self-execution,) (e.g., Catmur et al., 2007). That is, the development of a stronger intrapersonal stimulus-response association, which was formed from visual feedback of the observers' own movement, coincides with the updating of an internal model of the person's own action and the predicted sensory consequences. To this end, the passive observation of other-generated action elicits a smaller primed response effect following intrapersonal training because there is now an absence of the physical execution and associated 'efference copy', which was once a feature of the observed movement.

Indeed, the current instance of sensorimotor training that resulted in decreased corticospinal excitability during action-observation was likely related to the updating of the internal models of action. That is, the generation of one's own movement is coincident with the generation of an 'efference copy', which in turn, accommodates a forward model of the predicted sensory consequences. When these predicted sensory consequences are matched to the actual sensory consequences, then the observer will judge the action to be a result of their own motor commands (Blakemore et al., 2000). Following this model of motor control, researchers have striven to understand how the internal models of action can be updated by sensorimotor training (e.g., Hayes et al., 2012a, b; Ong & Hodges, 2010). In addition, evidence from intentional binding, which is suggested to reflect the sense of agency, shows an increased tendency to bind the perceived occurrence of self-generated action (reafference) and its subsequent stimulus event (external afference) following a period of stimulus-response training (Moore, Dickinson et al., 2011; Moore, Wegner et al., 2009). Therefore, in the context of the current study, it is possible the sensorimotor experiences and the associated updating of the internal model may enrich the observers' awareness of self-generated action, and with it, the distinction from 'other' observed actions. Interestingly, this effect was found

only in the condition in which the participants had received visual feedback of their own movement.

Consistent with the ideas discussed previously, and the fact that the modulation of corticospinal excitability was specific to the presence of visual feedback, we have recently found that interpersonal motor interference found during a behavioural task is contingent upon intrapersonal experiences consisting of visual feedback. Specifically, it is shown that the movement execution errors arising from the observation of incongruent compared to congruent movements begins to decrease following a period of training with visual feedback of the observer's own limb movements (Roberts et al., 2016). Meanwhile, training without visual feedback failed to decrease the motor interference effect. In the context of these findings, it appears that the external visual afference was required to couple with the efferent and reafferent sources of information during sensorimotor training. Presumably, the increased exposure to visual feedback refined an internal model of action that became more dependent upon the presence of vision (see also, Khan et al., 1998; Proteau et al., 1987).

Of note, the present findings lend strong support to the notion of modulating prime response effects following potential changes to the awareness of self- and other-generated actions. Indeed, previous evidence indicates that the tendency to execute faster motor responses (e.g., index finger lifting) when observing congruent (e.g., index finger lifted) compared to incongruent (e.g., middle finger lifted) action stimuli may be attenuated by an increased self-related focus (manipulated by the presence of a mirror that reflected an image of the observers' own hand) (Spengler, Brass, Kuhn, & Schutz-Bosbach, 2010; see also, Wang & Hamilton, 2013). These modulation effects have been attributed to neural regions associated with social cognition including the rTPJ and mPFC. Indeed, a decrease in automatic imitation has also been indicated following anodal (excitatory) direct current stimulation of the rTPJ (Santesteban, Banissy et al., 2012), while inversely increasing

following a virtual lesion of the rTPJ (using repetitive TMS (rTMS)) (Sowden & Catmur, 2015). Moreover, these same regions have been attributed to the distinction between self and other-generated actions (Brass et al., 2009; Spengler, von Cramon, & Brass, 2009).

Therefore, in the context of the present study, it may be the modulation of corticospinal responses following sensorimotor training resulted from the mediation of neural regions associated with social cognition (rTPJ, mPFC) as the observer became more aware of their own and other-generated actions.

To summarise, the present study found that the increase in corticospinal activity during action-observation can be attenuated by intrapersonal sensorimotor training with visual feedback of the observers' own movement. We suggest that this decrease may have been a consequence of the observer accruing an internal model of self-generated action, which accommodated the distinction between self-generated actions and 'other' observed actions. To our knowledge, this is one of the first studies to indicate that intrapersonal sensory-specific (i.e., visual) associative learning may be used to inversely inhibit a primed response following action-observation. The present findings differ from previous evidence of associative learning causing an enhanced primed response effect. This difference may be because of the nature of the stimulus-response training adopted within the present study, where the observers received feedback of their own movements. Such modulation would make intuitive sense for self-generated action as the training of one's own movements can help foster independent and accurate execution within social contexts by attenuating the potentially deleterious effects that may emerge from other people's actions (i.e., motor interference). Future research may wish to elaborate on these suggestions by examining the influence of stimulus-response training from both self- and other-generated actions on primed response effects including, but not limited to, automatic imitation.

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Figure Captions

Figure 1. Illustration of the visual stimuli and experimental procedure. Participants were assessed for their corticospinal excitability following the observation of action postures (*baseline, post-training*). The stimulus initially featured an image of a static hand followed by the presentation of an index and little finger abduction posture, which evokes the impression of apparent human movement. Participants would then train by continually abducting their index and little finger with (as indicated by the colour image) or without (as indicated by the greyscale image) visual feedback (*training*). The assignment of visual feedback conditions to each finger was counter-balanced across the participant pool.

Figure 2. Mean MEP ratio for the observation of congruent and incongruent action stimuli as a function of phase (baseline, post-training) and vision training (vision, no vision). Error bars represent the positive and negative standard errors for the congruent and incongruent conditions respectively.

Footnotes

1. Since the participants completed the two training protocols within the same session (i.e., vision and no vision training), there is the possibility that overall resting corticospinal excitability may have changed as result of the order in which the training conditions were received. Thus, we conducted a further analysis that incorporated a between-measures factor of order into the main omnibus ANOVA: order (vision first, no vision first), phase (baseline, post-training), congruency (congruent, incongruent), vision training (vision, no vision). There was no significant main, $F(1, 17) = 0.56$, $MSE = 0.069$, $p = 0.47$, $partial \eta^2 = .03$, or interaction effects (order x congruency: $F(1, 17) = 3.72$, $MSE = 0.01$, $p = 0.07$, $partial \eta^2 = .18$, order x phase x vision training: $F(1, 17) = 1.85$, $MSE = 0.034$, $p = 0.19$, $partial \eta^2 = .10$, remaining order effects: $F_s < 1$) that featured the factor of order. As a result, we presume there to be little or no influence of the time of delivering the two forms of training protocols on resting corticospinal excitability.
2. To ensure the background EMG (i.e., corticospinal activity) did not confound the main MEP results, we analysed the mean pre-activation (-50 ms) RMSE scores in a similar manner to our main analysis. That is, RMSE scores during the pre-stimulation period were submitted to a repeated-measures ANOVA featuring factors of phase (baseline, post-training), congruency (congruent, incongruent) and vision training (vision, no vision). The results of this analysis did not reveal any significant main, or interaction effects (congruency x vision: $F(1, 18) = 2.42$, $MSE = 0.010$, $p = 0.14$, $partial \eta^2 = .12$, phase x congruency x vision: $F(1, 18) = 2.11$, $MSE = 0.011$, $p = 0.16$, $partial \eta^2 = .11$, remaining statistical effects: $F_s < 1$). As a result, there was no indication of a confounding influence of background EMG and increased corticospinal activity when the participant was supposed to be at rest.