

Title: The modulation of motor contagion by intrapersonal sensorimotor experience

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Abstract

Sensorimotor experiences can modify the internal models for action. These modifications can govern the discrepancies between predicted and actual sensory consequences, such as distinguishing self- and other-generated actions. This distinction may also contribute toward the inhibition of movement interference, which is strongly associated with the coupling of observed and executed actions. Therefore, movement interference could be mediated by the sensorimotor experiences underlying the self-other distinction. The present study examined the impact of sensorimotor experiences on involuntary movement interference (*motor contagion*). Participants were required to complete a motor contagion paradigm in which they executed horizontal arm movements while observing congruent (horizontal) or incongruent (vertical) arm movements of a model. This task was completed before and after a training protocol in which participants executed the same horizontal arm movements in the absence of the model stimuli. Different groups of participants trained with or without vision of their moving limb. Analysis of participants who were predisposed to motor contagion (involuntary movement interference during the observation of incongruent movements) revealed that the no vision group continued to demonstrate contagion at post-training, although the vision group did not. We propose that the vision group were able to integrate the visual afferent information with an internal model for action, which effectively refines the ability to match self-produced afferent and efferent sources of information during response-execution. This enhanced matching allows for a better distinction between self and other, which in turn, mediates the inhibition of motor contagion.

Keywords:

motor contagion; sensorimotor experience; response-produced feedback; agency; inhibition

Introduction

The mimicry of observed motor behaviours has been suggested to unfold because of a common relation between the neural codes representing actions and their sensory consequences [1, 2]. Because of this perception-action coupling, the observation of action can activate the neural codes that are responsible for the execution of corresponding action. This motor system activation increases the potential for observed actions to be executed by the observer; a concept referred to as *motor contagion* [3]. It is thought that this common coding can be empirically observed by the interference caused by observing movements incongruent to our own executed movements [4]. Neurophysiological and neuro-imaging techniques have indirectly traced these behavioural outcomes to premotor and fronto-parietal regions of the human brain [5, 6]. This neural substrate seems to adhere to principles of Hebbian learning [7], and Associative Sequence Learning (ASL) theory [8, 9], which highlights the formation of stimulus-response links via sensorimotor experience. That is, by repeatedly executing a movement, the motor codes representing the action and the sensory consequences of the action become refined and coupled [10]. In support of this experience-dependent coupling between perception and action, the interference on executed arm movements (e.g., horizontal) (as indicated by involuntary movement variance) caused by observing an incongruent movement (e.g., vertical) may increase after physical practice of the observed (e.g., vertical) movement [11]. Relatedly, the facilitation of congruent actions can be eliminated through short-term incongruent stimulus-response training in which the observer executes an alternative action to that being observed (e.g., close hand response execution following open hand observation) [12, 13]. This incongruent sensorimotor training has been traced to the neural regions underlying typical (or congruent) mirror responses (premotor cortex, inferior parietal lobule; [15, 16]).

There has been a growing interest in the inhibition of contagion. This inhibition may be governed by the medial prefrontal cortex and the temporo-parietal junction [17]; areas strongly related to social cognition [18]. It is proposed that these regions accommodate a distinction between self- and other-generated behaviours (see [19] for a review). Changes in the ability to distinguish between self- and other-generated behaviours could mediate the amount of contagion exhibited by the observer. For example, Cook and Bird [20] showed the initial priming of a prosocial attitude enhanced the mimicry of observed actions. The prosocial prime was proposed to have “blurred” the distinction between self and other, which caused a greater relation between observed and executed actions, and thus, generated contagion.

The distinction between self and other may also be drawn from lower-level processes. That is, the distinction may be determined by a discrepancy between the predicted and actual sensory consequences of executed actions [21] (see also [22]). A match between the predicted and actual sensory consequences leads one to conclude that they were responsible for the action, whereas a mismatch leads to the attribution of “other” sources. The predicted sensory consequences are driven by an internal model that can be updated through sensorimotor experience [10, 23, 24]. It is through repeated experience of the action and its subsequent outcomes that the performer can couple physical reafferent signals with the visual sensory consequences. To elucidate, using the ‘intentional binding’ paradigm (see [25]), where the performer binds the perceived time of an executed action and the subsequent stimulus event, researchers have quantified the distinction between self and other (also referred to as ‘sense of agency’). Of interest, it has been shown that exposure to stimulus information that is contingent upon an executed action (e.g., auditory tone following a finger response) can enhance intentional binding, and with it, the sense of agency [26]. Therefore, it is possible that in the absence of response-produced visual feedback, the motor events are rendered

independent of the sensory events. In this situation, the predicted sensory consequences generated from the efference copy may be restricted to non-visual sources of afferent information. Consequently, the ability to distinguish between self- and other-generated actions based on response-produced visual information would be increased in someone trained with visual feedback of their own limb compared to without visual feedback, which would result in differences in the coupling of observed and executed actions, along with the incidence of motor contagion. In other words, the more an individual experiences a specific sensorimotor coupling, the more likely a self-other distinction will occur and contagion will be reduced.

With this in mind, the present study was designed to examine how different sensorimotor experiences affect motor contagion. To this end, we employed a test-retest design in which participants executed cyclical horizontal arm movements during the observation of congruent (horizontal) or incongruent (vertical) movements. Contagion was indicated by an increase in movement variance in the unintended orthogonal (vertical) axis of movement during the observation of incongruent compared to congruent movements. Because this study examined the experience-dependent inhibition of contagion, it was imperative that the participants of interest were initially susceptible to contagion (e.g., [4]). During training, the participants executed horizontal arm movements either with or without vision. If response-specific visual-motor codes developed through sensorimotor experience help to distinguish self- and other-generated actions, which in turn, accommodate the inhibition of motor contagion, then less contagion would be observed after training for the group trained with vision. Meanwhile, if the absence of response-produced visual feedback causes self- and other-generated actions to appear less distinct, then contagion would continue to unfold for the group trained without vision. Although these predictions seem to conflict with the lower-level sensorimotor theories of imitation which generally predict

sensorimotor experiences to enhance contagion (e.g., ASL), the present set of predictions are simply alternative outcomes based on the same stimulus-response mechanism. Whereas the sensorimotor experiences that are congruent with the observed stimulus have received most of the attention (e.g., [11]), the present study pertains to sensorimotor experiences of trained movements that are incongruent with the observed stimulus.

Method

Participants

Thirty-five participants (age range = 19-29 years) were randomly assigned to one of two groups (vision n=18, no vision n=17). All participants were self-declared right-handed, had normal or corrected-to-normal vision, and were compensated \$10 (CAD). The experimental procedures were approved by the Office of Research Ethics at the University of Toronto and conducted in accordance with the ethical guidelines and standards of the 1964 Declaration of Helsinki.

Apparatus, stimulus, task and procedure

The visual stimulus was displayed on a blank wall via a projector (Dell 1510X) at a viewing distance of 1.9 m. The experiment was controlled using PsychoPy [27] from a host PC with a spatial resolution of 1024 x 768 pixels, and refresh rate of 85 Hz. The stimuli were 30 s videos of a female adult executing straight-line cyclical horizontal (i.e., left (right)-right (left)) arm movements with an orthogonal (vertical) movement variance of 25.53 mm or vertical (i.e., up (down)-down (up)) arm movements with an orthogonal (horizontal) movement variance of 12.98 mm. The individual segments from each of the movement cycles were displaced at approximately 500 mm, and executed at a cycle rate of 0.5 Hz. The

size of the visual stimuli was scaled so the individual segments of the model subtended a 500-mm amplitude for the participant's own movement.

Participants stood 1.9 m from the stimulus display and executed horizontal arm movements similar to the horizontal model stimulus. Prior to data collection, participants became familiar with the horizontal arm movements with the aid of two targets placed on the wall 1350 mm apart (to scale with the prerequisite 500-mm executed amplitude). The movements were paced by an auditory metronome presenting stimuli at 1 Hz. Participants were to execute one arm movement segment/half-cycle per auditory tone (an actual execution rate of 0.5 Hz). The sensorimotor conditions of this initial familiarization phase were similar to the vision training condition because participants could see the movement of their limb. Following sufficient practice (typically 1 or 2 trials), the targets and metronome were removed and participants progressed to the experimental phase.

The experimental procedure followed a test-retest protocol. Participants completed 30-s trials in which they executed the criterion horizontal movement in-time with the video stimulus that was either congruent (horizontal) or incongruent (vertical) to the model's movement direction. Both the observed stimulus and executed arm movement could be clearly seen by the participants. There were four (2 congruent, 2 incongruent) trials at each of the pre-test and post-test phases, and the presentation order was randomized.

Following the pre-test trials, participants completed the training phase where they executed the same horizontal arm movements without the stimulus display. The vision group was instructed to observe their own arm throughout each trial and the no vision group had their vision occluded. Participants were reminded to try to uphold the criterion horizontal movement amplitude and cycling frequency. There were 15 training trials. A short break was offered after every two trials. Mandatory breaks were issued at the completion of each phase (i.e., pre-test/training/post-test).

Data recording, dependent measures and analysis

Movements at test phases were recorded via a small infrared sensor attached to the index finger of the executing limb using the 3D Investigator Motion Capture System (Northern Digital Inc., ON, Canada) sampling at 200 Hz. Position data were filtered at 10 Hz using an autoregressive filter implemented in MATLAB. Both the first and last 5 s were removed from the data to minimise any initial asynchrony between observed and executed movements and discard potential inattention or muscular fatigue effects, respectively [28]. Next, movement reversals in the primary axis of movement were identified by the signed change of frame-by-frame differences. The variances of fingertip position in the orthogonal (vertical) axis of movement were then calculated from each individual movement segment. The median of these variance scores were then taken in each individual trial. We removed trials from participants' data in which the movement variance exceeded 2.5SDs from the within-participant mean movement variance (2.54% of all trials). Participant mean scores that were above or below 2.5SDs away from the grand mean were also removed.

Because we were interested in understanding the influence of training in different sensorimotor conditions on motor contagion, the final analysis only included individuals who demonstrated contagion effects in the pre-test (defined as movement variance that was numerically larger for the incongruent compared to congruent trials; i.e., $\text{incongruent} - \text{congruent} > 0$; see [13]). Variance scores were submitted to a 2 (Vision: Vision, No Vision) by 2 (Test: Pre-test, Post-test) by 2 (Congruency: Congruent, Incongruent) mixed ANOVA with Vision as a between-participant factor, and Test and Congruency as within-participant factors. Any statistical interactions were further decomposed using simple interaction and main effect analyses respectively. Significance was declared at $p < .05$.

Results

There were 12 participants (8 vision group, 5 no vision group) that failed to show contagion at pre-test, and were thus eliminated from the data set.¹ A further one participant from the vision group was removed because their mean movement variance was more than 2.5 SDs from the grand mean. In the end, there were 9 participants in the vision group and 12 participants in the no vision group.

There was a significant main effect congruency, $F(1, 19) = 19.54, p < .001, \text{partial } \eta^2 = .51$, indicating greater variance for the incongruent compared to congruent condition. This effect was superseded by significant two-way interactions between vision and congruency, $F(1, 19) = 5.54, p < .05, \text{partial } \eta^2 = .23$, and test and congruency, $F(1, 19) = 17.89, p < .001, \text{partial } \eta^2 = .49$. There was no significant three-way interaction between vision, test and congruency, $F < 1$. Simple interaction analyses at each level of test (i.e., pre-test and post-test) revealed a significant effect of congruency, $F(1, 19) = 57.54, p < .001, \text{partial } \eta^2 = .75$, and no significant interaction between vision and congruency, $F(1, 19) = 3.64, p > .05, \text{partial } \eta^2 = .16$, at pre-test (Fig. 1). There was no significant main effect of congruency, $F(1, 19) = 2.57, p > .05, \text{partial } \eta^2 = .12$, although there was a significant interaction between vision and congruency, $F(1, 19) = 8.91, p < .01, \text{partial } \eta^2 = .32$, at post-test. This result indicated that there was greater variance in the incongruent compared to congruent condition (i.e., a contagion effect) for the no vision group, $F(1, 19) = 12.29, p < .01, \text{partial } \eta^2 = .39$, but no difference for the vision group, $F < 1$. Indeed, from the 12 no vision participants that initially demonstrated contagion at pre-test, there were 10 (83.33%) that continued to exhibit contagion (i.e., incongruent > congruent) at post-test. In contrast, from the 9 vision participants that demonstrated contagion at pre-test, there were only 4 (44.44%) that showed contagion at post-test. Furthermore, using separate paired-sample t-tests on incongruent trials for the vision and no vision groups, we also confirmed that there was a significant decrease

from pre-test to post-test in movement variance for the vision group, $t(8) = 2.72$, $p < .05$, $d = .66$. This was not the case for the no vision group, $t(11) = 1.28$, $p > .05$, $d = .39$. Thus, training with vision of the limb appeared to eliminate the contagion effect while training without vision did not.

Insert Figure 1 about here

Discussion

The current study examined the influence of different sensorimotor experiences on motor contagion. More precisely, we modulated the specific sensory information coupled to the motor events during training and examined how this coupling affected the performer's own movements. It was found that sensorimotor training featuring visual feedback of the limb assisted the performer in inhibiting contagion, but training without visual feedback continued to manifest contagion. These influences of training on contagion are specifically related to individuals that demonstrate inherent levels of contagion.

In part, these findings support the ASL theory because the visual sensory consequences from sensorimotor experiences can facilitate motor responses during the observation of trained movements [12]. To elucidate, movement deviation during the observation of incongruent movements (e.g., vertical) becomes even greater following training in the corresponding set of incongruent movements (e.g., vertical) [11]. However, the present study does not address the excitatory links responsible for increasing contagion by observing trained movements, but instead, the inhibition of contagion by observing untrained movements. That is, movement deviation during the observation of incongruent movements (i.e., vertical) becomes lower following training in an alternative set of congruent movements (i.e., horizontal).

In addition, this is one of the first studies to study ASL through sensorimotor experiences pertaining to external afferent signals generated by the performers themselves. Many studies related to ASL have adopted incongruent or counter-mirror training procedures featuring *interpersonal* observation-execution, although one of the key predictions involves relating sensory and motor events following *intrapersonal* observation-execution [32]. For example, infants may begin to mimic manual behaviours following increasing use and observation of their own hands (e.g., [33]). Although the current findings reflect the general role of sensorimotor experience, further investigation is needed to determine the properties of the visual information coded in training. Indeed, the inhibition may result from coding the observed spatial parameters (e.g., left and right in the horizontal) and/or the movement kinematics [34]. Once more, it is possible that the visual feedback of the limb during training helped participants to pay more attention to their own movements at post-test. Indeed, the inhibition of mimicry behaviour has also been suggested to manifest from the input or perceptual stage of processing, which can be influenced by attention [35].

Of interest, it has previously been shown that motor training without visual feedback can enhance the recognition of observed motor behaviours [36]. That is, there was better recognition of an observed movement pattern following training of the same pattern without response-produced visual feedback. Consequently, it was suggested that the mirror-matching mechanism within the human brain, and underlying the recognition of biological motion, is primarily dependent upon motor efference. Indeed, this is pertinent to the understanding of our current findings because the mirror-matching mechanism assumed to underlie observed biological motion is also associated with behavioural outcomes including motor contagion ([3, 37]. Although the contrast to the findings of our study remains elusive, we suggest training with vision has the greatest impact in our study because the interpersonal nature of the motor contagion paradigm assumes continuous coupling between observed and executed

actions. Alternatively, visual feedback was perhaps unnecessary for the visual recognition of observed actions in the Casile and Giese [36] study because there may have been a number of other cognitive factors contributing to performance. For example, the recognition of action may be greatly informed by the knowledge of unfolding temporal events, independent of the observed topographical and motion features ([38]). Indeed, it would be interesting to explore whether sensorimotor training featuring visual feedback, as in our study, manifests an additive impact on the visual recognition of biological motion.

The importance ascribed to sensorimotor experience to the inhibition of motor contagion may correspond with the sensorimotor experience related to distinguishing self- and other-generated actions. That is, the inhibition of contagion relates to the ability to distance oneself from others [18, 39]. This distinction is mediated by the comparison of the predicted and actual sensory consequences [21], which are built upon by the sensorimotor experiences accumulated in novel sensorimotor learning [11, 23, 29]. This conjecture is supported by evidence of enhancing self-other distinction following stimulus-response associative learning [26]. To elucidate, participants initially experienced an auditory tone stimulus that was contingent or non-contingent upon an executed action. The contingent condition caused participants to more closely bind the perceived time of an executed action and the auditory stimulus that was generated shortly after it. Thus, it elicited a greater sense of agency. With respect to the current findings, the sensorimotor experiences of the vision group may have accommodated the coupling of sensory and motor events for an increasing sense of agency, which in turn, mediated contagion.

Of interest, the sensorimotor experiences mediating inhibition were found only after training with vision, which indicates that the reafferent signals responsible for updating an internal model for action required the accompanying external visual afference. This finding is consistent with evidence from the manual aiming literature in which extended training with

visual feedback improves both movement planning and online limb control [40, 41]. Moreover, this sensory-specific training actually disadvantaged participants when they were required to execute under open-loop/no vision conditions. Thus, training with vision appeared to have enhanced the representation of the trained manual response by integrating the external visual afference. Presumably, the vision training condition in the current study specifically refined an internal model that was contingent upon the presence of visual feedback.

Recent evidence surrounding the inhibition of motor contagion has been strongly linked to neural regions involved in social cognition [17]. However, it remains to be seen how these regions are related to the current evidence of sensorimotor experiences underpinning inhibition. To this end, we draw on recent neuro-imaging evidence indicating that the social neural network closely interacts with the inferior frontal mirror regions during the interpretation [42] and mimicry [43] of observed human movements. In the context of the current findings, it may be the coupling of sensory and motor events accumulated in training elaborates on a sensorimotor representation, which helps to distinguish self- and other-generated actions within the mirror regions of the brain (inferior frontal cortex). As a consequence, this information may be forwarded to the top-down social regions (medial prefrontal cortex, temporo-parietal junction) associated with inhibition.

Conclusion

The present study revealed exposure to response-produced visual feedback during intrapersonal sensorimotor training aided the inhibition of motor contagion. In the absence of this feedback, contagion continued to unfold. This finding indicates the importance of sensorimotor experiences for the mediation of inhibition, perhaps via an increasing distinction between self- and other-generated actions. Because these findings were restricted

to a sub-set of individuals that were initially susceptible to contagion, it is of interest whether similar findings can be reflected in alternative paradigms with potentially more salient mimicry effects (e.g., [13]). Finally, these findings may have implications for the treatment of echopraxic symptoms and related disorders (e.g., [44]).

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References

- [1] Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (2001). The Theory of Event Coding (TEC): a framework for perception and action planning. *Behav Brain Sci*, 24(5), 849-878. doi: 10.1017/S0140525x01000103

- [2] Prinz, W. (1997). Perception and action planning. *European Journal of Cognitive Psychology*, 9(2), 129-154. doi: 10.1080/713752551

- [3] Blakemore, S. J., & Frith, C. (2005). The role of motor contagion in the prediction of action. *Neuropsychologia*, 43(2), 260-267. doi: 10.1016/j.neuropsychologia.2004.11.012

- [4] Kilner, J. M., Paulignan, Y., & Blakemore, S. J. (2003). An interference effect of observed biological movement on action. *Curr Biol*, 13(6), 522-525. doi: 10.1016/S0960-9822(03)00165-9

- [5] Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annu Rev Neurosci*, 27, 169-192. doi: 10.1146/annurev.neuro.27.070203.144230

- [6] Van Overwalle, F., & Baetens, K. (2009). Understanding others' actions and goals by mirror and mentalizing systems: a meta-analysis. *Neuroimage*, 48(3), 564-584. doi: 10.1016/j.neuroimage.2009.06.009

- [7] Keysers, C., & Perrett, D. I. (2004). Demystifying social cognition: a Hebbian perspective. *Trends Cogn Sci*, 8(11), 501-507. doi: 10.1016/j.tics.2004.09.005

- [8] Heyes, C. (2001). Causes and consequences of imitation. *Trends Cogn Sci*, 5(6), 253-261.
doi: 10.1016/S1364-6613(00)01661-2
- [9] Ray, E., & Heyes, C. (2011). Imitation in infancy: the wealth of the stimulus. *Dev Sci*, 14(1), 92-105. doi: 10.1111/j.1467-7687.2010.00961.x
- [10] Elsner, B., & Hommel, B. (2001). Effect anticipation and action control. *J Exp Psychol Hum Percept Perform*, 27(1), 229-240. doi: 10.1037//0096-1523.27.1.229
- [11] Capa, R. L., Marshall, P. J., Shipley, T. F., Salesse, R. N., & Bouquet, C. A. (2011). Does motor interference arise from mirror system activation? The effect of prior visuo-motor practice on automatic imitation. *Psychol Res*, 75(2), 152-157. doi: 10.1007/s00426-010-0303-6
- [12] Heyes, C., Bird, G., Johnson, H., & Haggard, P. (2005). Experience modulates automatic imitation. *Brain Res Cogn Brain Res*, 22(2), 233-240. doi: 10.1016/j.cogbrainres.2004.09.009
- [13] Press, C., Gillmeister, H., & Heyes, C. (2007). Sensorimotor experience enhances automatic imitation of robotic action. *Proc Biol Sci*, 274(1625), 2509-2514. doi: 10.1098/rspb.2007.0774
- [14] Catmur, C., Walsh, V., & Heyes, C. (2007). Sensorimotor learning configures the human mirror system. *Curr Biol*, 17(17), 1527-1531. doi: 10.1016/j.cub.2007.08.006

- [15] Catmur, C., Gillmeister, H., Bird, G., Liepelt, R., Brass, M., & Heyes, C. (2008). Through the looking glass: counter-mirror activation following incompatible sensorimotor learning. *Eur J Neurosci*, 28(6), 1208-1215. doi: 10.1111/j.1460-9568.2008.06419.x
- [16] Press, C., Catmur, C., Cook, R., Widmann, H., Heyes, C., & Bird, G. (2012). FMRI evidence of 'mirror' responses to geometric shapes. *PLoS One*, 7(12), e51934. doi: 10.1371/journal.pone.0051934
- [17] Brass, M., Ruby, P., & Spengler, S. (2009). Inhibition of imitative behaviour and social cognition. *Philos Trans R Soc Lond B Biol Sci*, 364(1528), 2359-2367. doi: 10.1098/rstb.2009.0066
- [18] Spengler, S., von Cramon, D. Y., & Brass, M. (2010). Resisting motor mimicry: control of imitation involves processes central to social cognition in patients with frontal and temporo-parietal lesions. *Soc Neurosci*, 5(4), 401-416. doi: 10.1080/17470911003687905
- [19] Sowden, S., & Shah, P. (2014). Self-other control: a candidate mechanism for social cognitive function. *Frontiers in Human Neuroscience*, 8. doi: ARTN 78910.3389/fnhum.2014.00789

- [20] Cook, J., & Bird, G. (2011). Social attitudes differentially modulate imitation in adolescents and adults. *Exp Brain Res*, 211(3-4), 601-612. doi: 10.1007/s00221-011-2584-4
- [21] Daprati, E., Franck, N., Georgieff, N., Proust, J., Pacherie, E., Dalery, J., & Jeannerod, M. (1997). Looking for the agent: an investigation into consciousness of action and self-consciousness in schizophrenic patients. *Cognition*, 65(1), 71-86. doi: 10.1016/S0010-0277(97)00039-5
- [22] Jeannerod, M. (1999). The 25th Bartlett Lecture. To act or not to act: perspectives on the representation of actions. *Q J Exp Psychol A*, 52(1), 1-29. doi: 10.1080/713755803
- [23] Wolpert, D. M., & Flanagan, J. R. (2010). Motor learning. *Curr Biol*, 20(11), R467-472. doi: 10.1016/j.cub.2010.04.035
- [24] Wolpert, D. M., & Ghahramani, Z. (2000). Computational principles of movement neuroscience. *Nat Neurosci*, 3 Suppl, 1212-1217. doi: 10.1038/81497
- [25] Haggard, P., Clark, S., & Karogeras, J. (2002). Voluntary action and conscious awareness. *Nat Neurosci*, 5(4), 382-385. doi: 10.1038/n827
- [26] Moore, J. W., Lagnado, D., Darvany, C. D., & Haggard, P. (2009). Feelings of control: contingency determines experience of action. *Cognition*, 110(2), 279-283. doi: 10.1016/j.cognition.2008.11.006

- [27] Peirce, J.W. (2007) Psychopy – Psychophysics software in Python. *J Neurosci Methods*, 162(1-2), 8-13
- [28] Hardwick, R. M., & Edwards, M. G. (2012). Motor interference and facilitation arising from observed movement kinematics. *Q J Exp Psychol*, 65(5), 840-847.
doi:10.1080/17470218.2012.672995
- [29] Hayes, S. J., Andrew, M., Elliott, D., Roberts, J. W., & Bennett, S. J. (2012). Dissociable contributions of motor-execution and action-observation to intermanual transfer. *Neurosci Lett*, 506(2), 346-350. doi: 10.1016/j.neulet.2011.11.045
- [30] Romero, V., Coey, C., Schmidt, R. C., & Richardson, M. J. (2012). Movement coordination or movement interference: visual tracking and spontaneous coordination modulate rhythmic movement interference. *PLoS One*, 7(9), e44761.
doi:10.1371/journal.pone.0044761
- [31] Roberts, J. W., Bennett, S. J., & Hayes, S. J. (2015). Top-down social modulation of interpersonal observation-execution. *Psychol Res*. doi:10.1007/s00426-015-0666-9
- [32] Heyes, C. (2010). Where do mirror neurons come from? *Neurosci Biobehav Rev*, 34(4), 575-583. doi:10.1016/j.neubiorev.2009.11.007
- [33] Marshall, P. J., Bouquet, C. A., Thomas, A. L., & Shipley, T. F. (2010). Motor contagion in young children: Exploring social influences on perception-action coupling. *Neural Netw*, 23(8-9), 1017-1025. doi:10.1016/j.neunet.2010.07.007

- [34] Roberts, J. W., Hayes, S. J., & Bennett, S. J. (2015). Motor contagion: the contribution of trajectory and end-points. *Psychol Res*, 79(4), 621-329. doi: 10.1007/s00426-014-0589-x
- [35] Spengler, S., Brass, M., Kuhn, S., & Schutz-Bosbach, S. (2010). Minimizing motor mimicry by myself: self-focus enhances online action-control mechanisms during motor contagion. *Conscious Cogn*, 19(1), 98-106. doi:10.1016/j.concog.2009.12.014
- [36] Casile, A., & Giese, M. A. (2006). Nonvisual motor training influences biological motion perception. *Curr Biol*, 16(1), 69-74. doi: 10.1016/j.cub.2005.10.071
- [37] Press, C., Cook, J., Blakemore, S. J., & Kilner, J. (2011). Dynamic modulation of human motor activity when observing actions. *J Neurosci*, 31(8), 2792-2800. doi:10.1523/JNEUROSCI.1595-10.2011
- [38] Cook, R., Johnston, A., & Heyes, C. (2012). Self-recognition of avatar motion: how do I know it's me? *Proc Biol Sci*, 279(1729), 669-674. doi: 10.1098/rspb.2011.1264
- [39] Spengler, S., von Cramon, D. Y., & Brass, M. (2009). Control of shared representations relies on key processes involved in mental state attribution. *Hum Brain Mapp*, 30(11), 3704-3718. doi: 10.1002/hbm.20800

- [40] Khan, M. A., Franks, I. M., & Goodman, D. (1998). The effect of practice on the control of rapid aiming movements: evidence for an interdependency between programming and feedback processing. *Q J Exp Psychol*, 51A(2), 425-443. doi: 10.1080/713755756
- [41] Proteau, L., Marteniuk, R. G., Girouard, Y., & Dugas, C. (1987). On the type of information used to control and learn an aiming movement after moderate and extensive training. *Hum Mov Sci*, 6(2), 181-199. doi: 10.1016/0167-9457(87)90011-X
- [42] Spunt, R. P., & Lieberman, M. D. (2012). An integrative model of the neural systems supporting the comprehension of observed emotional behavior. *Neuroimage*, 59(3), 3050-3059. doi: 10.1016/j.neuroimage.2011.10.005
- [43] Wang, Y., Ramsey, R., & Hamilton, A. F. (2011). The control of mimicry by eye contact is mediated by medial prefrontal cortex. *J Neurosci*, 31(33), 12001-12010. doi:10.1523/JNEUROSCI.0845-11.2011
- [44] Brass, M., Derrfuss, J., Matthes-von Cramon, G., & von Cramon, D. Y. (2003). Imitative response tendencies in patients with frontal brain lesions. *Neuropsychology*, 17(2), 265-271. doi.org/10.1037/0894-4105.17.2.265

Figure captions

Fig. 1 Mean movement variance as a function of vision training, test and congruency (error bars represent standard errors).

Footnote

1. The failure to find baseline contagion in some individuals was unexpected, but may be due to a series of factors manifesting from individual differences including visual tracking of the stimulus [30] and/or primed social attitude [31]. Notably, this subset of participants indicated segment movement times close to the criterion ($M = 986.53\text{ms}$, $SE = 1.57\text{ ms}$), which would strongly suggest they followed instructions to move in-time with the stimulus.