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Eye movements may cause motor contagion effects

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Abstract

When a person executes a movement, the movement is more errorful while observing another person's actions that are incongruent rather than congruent with the executed action. This effect is known as "motor contagion". Accounts of this effect are often grounded in simulation mechanisms: increased movement error emerges because the motor codes associated with observed actions compete with motor codes of the goal action. It is also possible, however, that the increased movement error is linked to eye movements that are executed simultaneously with the hand movement because oculomotor and manual-motor systems are highly interconnected. In the present study, participants performed a motor contagion task in which they executed horizontal arm movements while observing a model making either vertical (incongruent) or horizontal (congruent) movements under three conditions: no instruction, maintain central fixation, or track the model's hand with the eyes. A significant motor contagion-like effect was only found in the 'track' condition. Thus, 'motor contagion' in the present task may be an artifact of simultaneously executed incongruent eye movements. These data are discussed in the context of stimulation and associative learning theories, and raise eye movements as a critical methodological consideration for future work on motor contagion.

Keywords: motor contagion, eye movements, simulation theory, joint action, action imitation

Eye movements may cause motor contagion effects

During many acts of daily living, individuals complete their own tasks while watching and coordinating their actions with the actions of other people. The influence that one person's (the model) movements have on the characteristics of another person's (the actor) movement has been investigated using a number of different paradigms. Action imitation effects (see Heyes, 2011 for a review) are often explained in terms of observation-evoked simulation (Kilner, Paulignan, & Blakemore 2003). That is, observing a model's actions leads to the automatic activation of motor codes associated with the observed response in the observing actor which subsequently influences the actor's movement execution (Blakemore & Frith, 2005; Jeannerod, 2001). Such observation-evoked simulation can act in a facilitatory manner when observed and to-be-executed movements are consistent with one another, as in automatic imitation effects like visuomotor priming. Alternatively, simulation can interfere with motor production resulting in larger variance (error) in the executed movement when the observed action is incongruent to the individual's intended action. This latter 'interference' effect, termed motor contagion, is the topic of the present paper.

Motor contagion (Kilner, Hamilton, & Blakemore, 2007; Kilner et al., 2003) is commonly investigated by having an actor make cyclical movements along one plane while observing a model make similar actions along the same (congruent) or orthogonal (incongruent) plane. For example, actors may make horizontal arm movements while observing a model make horizontal or vertical arm movements. Movement variance along the orthogonal (i.e., vertical) axis to the intended (i.e., horizontal) movement is then calculated giving an index of 'motor contagion' or interference (cf. Richardson, Campbell, & Schmidt 2009). Consistent with the notion that the motor contagion effect is dependent on a social neural network in which the observed actions of the model are activated and simulated in the participant, such interference effects are often absent when the stimulus is not human-like

(Kilner et al., 2003) or the stimulus follows a biologically implausible velocity profile. In contrast, the interference effects are present when an abstract or robotic stimulus follows a biologically plausible velocity profile or participants believe in the human agency of the stimulus (see, Kilner et al., 2007; Roberts, Hayes, Uji, & Bennett 2015; Stanley, Gowen, & Miall 2007).

In these studies, however, little or no attention has been given to how the actor's eye movement may influence action execution. In fact, actors are often instructed to follow the model's movements with their eyes while completing the task (e.g., Kilner et al., 2003). Such an instruction, or at minimum the lack of specific gaze instructions in subsequent studies, may influence the manual actions via eye-hand coupling mechanisms. It is well established that movement coding in eye and hand movement systems are tightly interconnected (e.g., Bekkering, Abrams, & Pratt 1995), and, during both action execution and observation, eye movements are predictive of hand action (the hand follows the eyes: e.g., Flanagan & Johansson, 2003; Land, 2006, 2009). In motor contagion paradigms, allowing, or even explicitly asking, actors to follow the hand movement of the model with their eyes may force their visuomotor system to alter executed hand movements. That is, executing cyclical vertical eye movements on incongruent trials might increase hand movement variance in that direction due to eye-hand coupling mechanisms, with or without the theorised simulation mechanism.

This line of thinking parallels research conducted in rhythmic movement interference paradigms that show eye-movements play a considerable role in cyclic movements coordinated with non-biological stimuli (see Romero, Coey, Schmidt, & Richardson 2012). Many motor contagion researchers, however, would argue that biological stimuli or other's actions are uniquely processed by a social network involving mirror neurons (Kilner & Lemon, 2013 for a short review on mirror neurons) or a similar coding system, and, as such,

may produce effects distinct from those investigated using rhythmic movement interference paradigms.

To directly investigate the role that eye movements may play a role in increased motor variability during the observation of incongruent biological movements, participants (actors) in the present study executed horizontal cyclic arm movements while observing a projection of a human model making either congruent (horizontal) or incongruent (vertical) movements. Participants completed the task under three conditions in separate blocks: no gaze instruction, fixation (fixate on a mark in the center of the projection), and track (follow the model's finger with your eyes). If the observation of action alone is critical and concurrently executed eye movements play a negligible role, then a motor contagion effect will be observed in all conditions. Conversely, if eye movements are implicated in the increased movement variability when participants observe incongruent relative to congruent movements, then a motor contagion-like effect will be observed only in the 'track' condition. That is, greater variance in movement along the orthogonal axis to the intended movement will be present in the incongruent condition as compared to the congruent condition when the actors are instructed to follow the models hand with their eyes.

Method

Participants.

Fourteen volunteers from the University of Toronto student community participated in the experiment in exchange for \$10 CA. All participants were between the ages of 18 and 30 years old, had normal or corrected-to-normal vision, gave informed consent and were right handed. Procedures were approved by the University of Toronto Office of Research Ethics.

Stimuli and Apparatus.

The stimuli were two videos of a Caucasian male adult executing horizontal (congruent stimulus) or vertical (incongruent stimulus) arm movements of approximately 500

mm amplitude at a rate of 0.5 Hz (complete cycle). The model wore a black t-shirt and sunglasses and had a motion capture marker attached to his finger. These videos were presented life-size on a white blank wall with a projector (Dell 1510X, Round Rock, Texas, USA). The stimulus presentation order was controlled via Python using Psychopy (Peirce, 2007). The movements were viewed at a 2.4 m distance and thus subtended approximately 12° of visual angle.

Participant's arm movements were recorded using an Optotrak 3D Investigator (Northern Digital Inc., Waterloo, Ontario, Canada) sampling at a rate of 200 Hz with one infrared wired sensor attached to the participant's right index finger. Vertical eye movements were recorded using an electrooculography (EOG) system, with one electrode above and one below the eye. EOG data was collected at a rate of 200 Hz using a UFI model 2122i Universal Bioamplifier (Morro Bay, California, USA) with the DC signal, filtered at .05Hz and 50 Hz. EOG produces a potential difference between the electrodes located above and below the eyes as the eye moves up and down (in this case). Hence, in the present experiment EOG provides a relative index of the position of the eye along the vertical plane.

Design and Procedure.

Prior to the experiment, participants practiced making horizontal cyclic movements between two points marked on a wall to ensure movements were the correct amplitude, frequency, and direction. Participants then made the same cyclic horizontal movements while observing the model making horizontal (congruent) or vertical (incongruent) movements. Participants completed three blocks of six trials, consisting of three congruent trials and three incongruent trials presented in random order. Participants always completed the 'no gaze instruction' condition first, in which they were simply asked to make cyclic horizontal movements in time with the actor (i.e., no specific eye movement instructions). This condition was completed first to provide a measure of unbiased or 'spontaneous' eye

movement behaviour and contagion. The order of the remaining two conditions were counterbalanced. In the ‘fixation’ condition, participants were asked to fixate on a central cross throughout the trial. In the ‘track’ condition, participants were asked to follow the model’s hand with their eyes throughout the trial. Each trial lasted 30 seconds. Participants were given a rest period after each trial to prevent fatigue. Participants in the Kilner et al. (2003) study also completed trials on which they made vertical movements in response to observed incongruent and congruent actions. Because Kilner and colleagues found the effects to be similar in the vertical condition, to simplify the design and allow participants to complete the trials without fatigue we did not include a vertical movement condition. Further, Kilner et al. compared movement variability in an incongruent condition against a baseline condition where participants observed no movements while executing their own cyclic movements. We used the congruent condition as our baseline because Kilner and colleagues found that this condition did not significantly differ from the baseline, and we were primarily interested in interference relative to a condition that retains an action observation component. These changes allowed us to increase the amount of data that was obtained for each condition to provide a more accurate estimate of the true effect while retaining the critical comparison.

Results

Two participants’ data were removed prior to analysis due to substantial marker recording errors—the markers were out of camera range from exaggerated or inappropriate movements). Both the first and last 5 s were removed from the arm and eye movement data to minimise errors due to asynchrony between observed and executed movements and discard potential inattention or muscular fatigue effects, respectively. After data processing, we subjected the data to Bayesian analysis using JASP (JASP Team, 2016) which, because we predicted a specific direction of effects, consisted of a series of one-tailed tests. We also

calculated 95 % confidence intervals for the differences in movement variance between congruent and incongruent conditions for both measures.¹

Eye Movements

The EOG signal was first filtered with a second order dual pass, Butterworth filter set at 10 Hz. The degree to which participants moved their eyes at the desired rate of 0.5 Hz was evaluated by analyzing the EOG signal on each trial in the frequency domain. First, any linear (i.e., DC) trend was removed from the EOG data. Second, a Fast Fourier Transform (FFT) was computed after applying a Hanning truncation window on the middle 3000 samples of a trial. A transform length of 4096 samples yielded a frequency resolution of 0.048 Hz. The output of the FFT was then converted into a log-transformed power spectra. This power spectra represented the degree to which specific oscillation frequencies contributed to the EOG signal. Based on the frequency resolution of the analysis, the closest frequency to the instructed rate of eye movements (i.e., 0.5 Hz) was 0.48 Hz. The log-power at this frequency was taken as an approximation of the degree to which participants' gaze was varying in the vertical direction at a rate of approximately 1 second per segment (i.e., 0.5 Hz cycles); or the degree to which participants were making vertical eye movements at the instructed rate.

The pattern of data from the EOG indicated that participants followed instructions. We calculated a difference score between incongruent and congruent trials for each condition (No instruction, Fixate & Track), and compared the difference score for each condition against a test value of 0. For both the No instruction and Fixate conditions, the model favoured the null hypothesis but only slightly. The data were 2.22 and 1.47 times, respectively, more likely under the null hypothesis. These values are indicative of inconclusive results (Jeffreys, 1962). In all likelihood, the differences between congruent and

¹ Data and analyses can be found on the Open Science Framework at <https://osf.io/uxezg/>.

incongruent conditions were too small to detect a difference. Indeed, confidence intervals span 0 for these two conditions: ‘no instruction’ (Mean congruent = 1.26; Mean incongruent = 1.37; Mean difference = 0.11, [-0.34, 0.57]), and ‘fixate’ (Mean congruent = 0.92; Mean incongruent = 1.15; Mean difference = 0.24, [-0.31, 0.78]) conditions. In sharp contrast, however, the data for the instruction condition were 202.42 times more likely under the alternative hypothesis that participants moved their eyes along the vertical plane more in the incongruent condition than in the congruent condition (Mean congruent = 0.98; Mean incongruent = 1.92; Mean difference = 0.94, 95 % CI[0.53, 1.34]). Thus, participants followed instructions.

Hand Movements

All data were subjected to a second-order dual pass Butterworth filter with a cut-off frequency of 10 Hz. On average across all conditions, participants’ movement times for one directional movement was 1000.64 ms (SD = 8.77 ms) suggesting that participants successfully synchronised their movements with the actor (No Instruction Congruent = 998.50 ms, No Instruction Incongruent = 1003.42 ms, Fixate Congruent = 999.43, Fixate Incongruent = 999.30, Track Congruent = 1001.11, Track Incongruent = 1001.18). The motor contagion effect was computed by subtracting average variance on congruent trials from the average variance on incongruent trials—with larger motor contagion effects being represented by larger positive numbers and smaller contagion effects being represented by values closer to “0”.

Given the a priori predictions that motor contagion effects should only occur in the ‘track’ condition (i.e., and not in the ‘fixate’ and ‘no instruction’ conditions), we first examined the difference in movement variability on congruent and incongruent trials for each instruction condition against the prediction that the difference would be greater than 0. Consistent with our hypothesis the no instruction and fixate conditions resulted in estimated

Bayes Factors of 4.39 (Mean difference = -2.31 mm, 95 % CI[$-16.91, 12.30$]) and 3.91 (Mean difference = -1.76 mm, 95 % CI[$-25.28, 21.76$]) in favour of the null hypothesis, respectively. That is, the data were more than three times likely to occur under the null hypothesis for both conditions. Conversely, the track condition resulted in a Bayes Factor of 8.18 in favour of the alternative hypothesis (Mean difference = 18.38 mm, 95 % CI[$4.23, 32.54$]; see Fig. 1). According to Jeffreys (1962), this is substantial (moderate) evidence for our hypotheses in all three cases. Further, changes in prior revealed posterior distributions in the same range of effects.

Given the marginal effects² in favour of the null hypothesis for the no instruction and fixate conditions we further explored the data to determine if the track condition resulted in a larger motor contagion effect than the two ‘null’ conditions. Our model, which predicted that directed eye movements are a critical factor in producing the motor contagion effect, was tested using Bayesian analysis. Our model specified that the ‘track’ condition would result in a larger motor contagion effect (larger positive values) than the ‘no instruction’ and the ‘fixate’ conditions, which were expected to result in the same distribution with an effect around 0. The results of the analysis were consistent with our hypothesis, with an estimated Bayes factor (null/alternative) of 0.19:1 in favor of the alternative hypothesis. In other words, the data are 5.31 more likely under the hypothesized model than the null hypothesis. This result is considered moderate evidence in favour of the alternative hypothesis that there would be larger movement variability in the track condition than in the other two conditions. Although we used a default uninformed prior width (.707), analysis revealed that the posterior distribution remained robust resulting in estimated Bayes Factors within the same range of effects.

² Bayes factors around 3 are roughly equivalent to $p = .05$.

Overall, the results of the Bayesian analyses and the confidence intervals provide converging evidence that motor contagion-like effects only emerged in the track condition. On the other hand, the no instruction and fixate conditions produced data that were more consistent with the null hypothesis though the effects could be considered to be marginal. Nevertheless, when the ‘motor contagion’ scores for no instruction and fixate conditions were compared against those of the track condition the distribution was found to be different and thus we conclude, at the very least, eye movements contribute to observed motor contagion like effects.

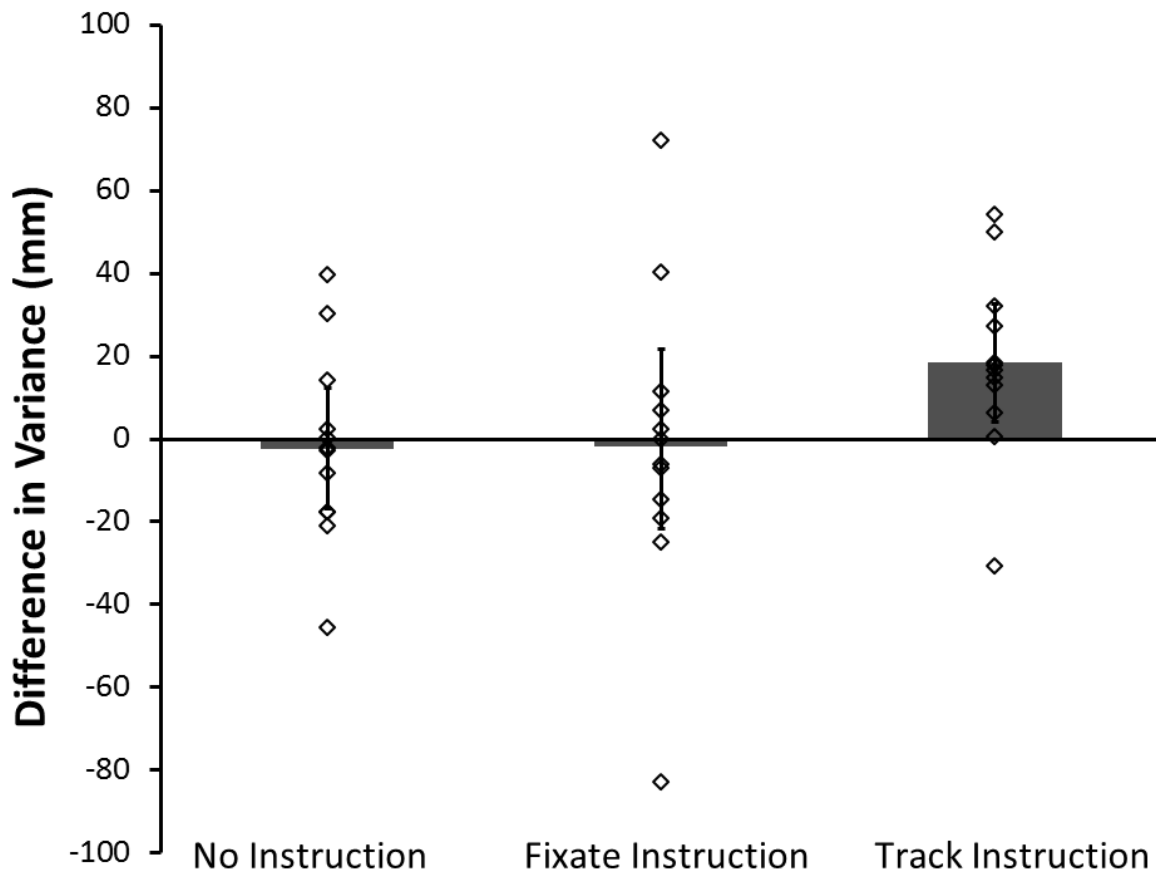


Figure 1. The difference in variance in millimeters between incongruent and congruent conditions for each type of instruction. Error bars represent 95% confidence intervals. Diamonds represent the average variance for an individual participant for each condition.

Discussion

The key finding from the present experiment was that differences in movement variance in the vertical direction between incongruent and congruent trials was found only when participants were given specific instructions to ‘track’ the hand of the model with their eyes. Notably, this condition was also the only one in which there were incongruent-congruent differences in the pattern of vertical eye movements. These findings indicate that participant instruction and subsequent eye movements drove the present motor contagion-like effect. Because motor contagion-like effects did not emerge in the conditions in which eye movements in the vertical (incongruent) direction were minimal (i.e., the fixate and no instruction conditions), the present data raise the strong possibility that eye movements made a meaningful contribution to the effects reported in other motor contagion studies; especially in studies in with similar ‘track’ instructions (e.g., Kilner, 2003). It is difficult to know the influence of eye movements relative to spontaneous tendencies to simulate the observed model’s action in previous work because the presence of concurrent eye movements is typically not reported in other studies. At minimum, the present data make it clear that concurrently executed eye movements are a critical consideration in the motor contagion paradigm.

It is possible that no contagion effects emerged in the fixate condition because the movement was not adequately processed. The movement might not have been processed in the fixate condition because the extreme ends of the movement landed in the peripheral visual field. However, it seems unlikely that this could account for a lack of contagion effect in this condition because the incongruent movements in the track condition would also land in the peripheral visual field (perhaps even more so). To elaborate, in the track condition participants were instructed to follow the hand with their eyes, thus their eyes remained fixated on the plane orthogonal to their movement. If lack of processing at the periphery was driving any effect then the fixate and the track conditions should have provided roughly

analogous results. Further, the timing of the movements was similar across conditions indicating that participants were still able to synchronize, and hence follow, the observed movement.

Instructions promoting eye movements that track the observed behavior may have artificially resulted in an interference effect in the present work for two reasons. First, there is an extensive literature on eye–hand coordination indicating that the eye and hand are coupled and the hand tends to follow the eye (e.g. Bekkering et al., 1995; and see Land, 2009 for a review). Thus, the vertical movement of the eyes in the incongruent condition may draw the hand into more vertical dispersion. Second, even if hand-to-eye coupling did not drive the effect (i.e., eye and hand movements can be planned and executed independently), instructed eye movement is unusual which might have caused increased movement variance. To clarify, it is unusual to solely track a stimulus while interacting with it (Land, 2009). Rather, the eyes fixate on predicted points along a stimulus' trajectory (e.g., Flanagan & Johansson, 2003). Therefore, asking a participant to deviate from a standard predictive gaze pattern oriented around their own interactions with the target stimulus may result in an interference effect because it is much more difficult to complete a task when the eyes are constantly moving and are not directed at the optimal location for such an interaction. Simply put, forcing people to constantly move their eye along the orthogonal plane of action disrupts the typical and stable source of visual information people use to ensure movement accuracy, creating more room for error.

It is also worth noting that restricting eye movements typically results in longer action execution with no decrement on actual performance (Ballard, Hayhoe, Li, & Whitehead 1992). This seems to directly be associated with the 'fixate' condition. However, one could speculate that it more so applies to the 'track' condition as the way in which participants were asked to execute their eye movements was highly constrained and perhaps required more

effort than a 'fixate' condition. So in the present case where temporal synchrony was the main goal of the task, rather than the spatial accuracy, participants may have compensated with lower kinematic precision (i.e., a spatial-temporal trade-off). These explanations can also account for findings that show an interference effect with abstract and non-biological stimuli (Bouquet, Gaurier, Shipley, Toussaint, & Blandin 2007; Jansson, Wilson, Williams, & Mon-Williams 2007; Romero et al., 2012); that is, an interference effect could simply be an artifact of eye-movements that have been elicited by various task constraints or participant instruction.

Such a simple eye-movement interference explanation can also account for the findings that suggest a dissociation between biological and non-biological stimuli (e.g. Kilner et al., 2003) if we assume that biological stimuli may increase an individual's propensity to 'track' a stimulus. Indeed, it is known that biological stimuli (Press, 2011), or simply bodily extremities such as the hands (Matarić & Pomplun 1998), encourage visual tracking. For example, Flanagan and Johansson (2003) reported that observers used different patterns of eye movements when watching a human or a robot move objects. Thus, with an increased propensity to track a biological stimulus, such stimuli would result in greater interference than non-biological stimuli in a motor contagion task because 'tracking' behavior may not be the most natural or efficient way of completing the task.

This brings us to our final point for future research. Humans perform complementary joint actions on a daily basis and they perform these actions with relative ease. Yet the motor contagion paradigm suggests interference. Perhaps such a tight theorised link between simulation and successful interactions is not warranted in all situations. Clearly, in the fixation condition of the present task, participants are still able to perform the timing task. Is simulation absent as suggested by the lack of interference? Or is it possible to engage simulatory mechanisms without interference? A third possibility involves a more adaptive

system (e.g. Cook, Bird, Catmur, Press, & Heyes 2014). Perhaps there are substantial gains to using simulatory mechanisms in some cases, as in paradigms investigating facilitatory effects (e.g., visuomotor priming, Bach & Tipper, 2007), but in the case of incongruent actions we quickly adapt to avoid interference based effects.

This present paper joins a growing body of literature calling for a critical evaluation of traditional simulation or representationally based interpretations of some phenomena associated with action understanding and joint coordination (e.g. Carr & Winkielman, 2014; Hickok, 2014; Press & Cook, 2015; Vannuscorps & Caramazza, 2016). Cook and colleagues (2014), for example, suggest that the mirror neuron system and, subsequently related phenomena, are borne out of associative learning and do not necessarily represent a hard-wired socially evolved system. Specifically, repeated pairings of sensorimotor experience (self and other action observation and execution) results in the automatic activation of motor codes in response to action observation. These associations can be strengthened, but they are also adaptive. Indeed, through training, motor activation can shift from congruent to incongruent actions (Catmur, Walsh, & Heyes 2007). Dialogue related to the idea of an associative learning account stresses the importance of an adaptable, context specific network that retains a level of social speciality (see commentaries on Cook et al., 2014). Although our findings do not directly speak to competing theories, the absence of interference in our data when controlling for eye movements cannot be situated within a theory that rigidly predicts simulation based interference when observing non-matching actions.

In conclusion, the motor contagion effect may be dependent upon, or modulated by, tracking with the eyes. Therefore, to enhance the ecological and internal validity of the tool when investigating motor interference effects associated with action observation careful consideration of eye movements is important. We strongly suggest that eye movements must be examined in relation to action observation and motor simulation in coordinative tasks as

they seem to be an integral contributor to how experimental effects do or do not manifest. Studies often cited within the motor contagion literature as being evidence of simulation interference may simply result from an increase in an individual's propensity to track a stimulus with their eyes and as such may be at least partially explained as an artifact of eye-hand coupling. Such eye-movements may or may not be linked to simulation. At minimum, it is clear from our study is that interference is not always present for complementary actions and it is imperative that researchers consider the role of eye movements when making methodological decisions to study the effects of action observation on movement execution.

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