ARE OBSERVED EFFECTS OF MOVEMENT SIMULATED DURING MOTOR IMAGERY PERFORMANCE?

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We have no known conflicts of interest to disclose. All data, analysis code, and research materials are available by emailing the corresponding author.

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ABSTRACT:

Motor learning relies on adjusting performance of movements via error detection and correction. How motor learning proceeds via motor imagery, the imagination of movement, is not understood. Motor imagery-based learning is thought to rely on comparing the predicted effect of movement, resulting from the forward model, against its intended effect. Whether motor imagery-based learning uses the observed effect of movement, simulated in motor imagery, to make comparisons to the intended effect to permit error detection and correction, is an open question. To address this, transcranial magnetic stimulation was used to inhibit the left inferior parietal lobe (L_IPL) after each trial of a task requiring participants to reproduce complex trajectories via motor imagery. From past work, we speculated the L_IPL was a candidate for integrating simulated feedback about task performance (simulated observed effects), hypothesizing inhibition of the L_IPL would impair learning, suggesting simulated observed effects of movement are used in motor imagery-based learning. Participants received stimulation to the L_IPL or over the vertex of the head after each trial. Learning was defined as reduced error on a repeated trajectory in comparison to randomly generated trajectories. Regardless of group participants learned, a finding countering our hypothesis, suggesting i) observed effects of movement are not simulated in motor imagery; ii) the L_IPL is not involved in integrating simulated observed effects of movement; or iii) the timing of the stimulation did not align with the speculated role of the L_IPL. Results encourage further research probing simulated feedback in motor imagery and its neural correlates.

KEYWORDS:

- Error
- Motor Imagery
- Motor Learning
- Movement
- Parietal Lobe

INTRODUCTION:

Acquisition of novel motor skills or improvement in performance of previously acquired skills occur via motor learning (Fitts & Posner, 1967; Newell, 1991). It is well accepted that motor learning proceeds through repeated execution of the motor skill to be acquired, with the identification and subsequent correction of errors ultimately resulting in better performance (Hardwick et al., 2013; Wolpert, 2014). This error detection/correction process is driven by neuroanatomical computations that minimizes the distance, error, between the state of the body and its environment (i.e., the observed effect of movement) and it's intended effect (i.e., the desired outcome of the movement; Blakemore et al., 2002; Dahm & Rieger, 2019b; Shadmehr et al., 2010; Shadmehr & Krakauer, 2008; Wolpert & Kawato, 1998). Figure 1A details a framework outlining these computations; an inverse model, the sensory to motor transformation that results in the motor command(s) necessary to achieve the intended effect, is first created (Blakemore et al., 2002; Dahm & Rieger, 2019b). Parallel to the motor command being sent to the effectors to execute the movement, a copy of the plan (i.e., the efference copy) is used by the forward model which outputs a prediction of the body's upcoming position (i.e., the predicted effect of movement) via a motor to sensory transformation (Wolpert & Flanagan, 2001). As the movement is executed the forward model integrates sensory information regarding the state of the body and its environment (i.e., observed effects) in real time, to update and adjust the forward model to minimize the difference (error) between the predicted effect (from the forward model) and the observed effect (Fig 1A, see circle 1; Shadmehr & Krakauer, 2008). Upon completion of the movement, the predicted and observed effect of movement are compared against the intended effect to identify and integrate adjustments to the motor command to improve performance on the subsequent trial (Fig 1A, see circles 2 and 3; Blakemore et al., 2002).

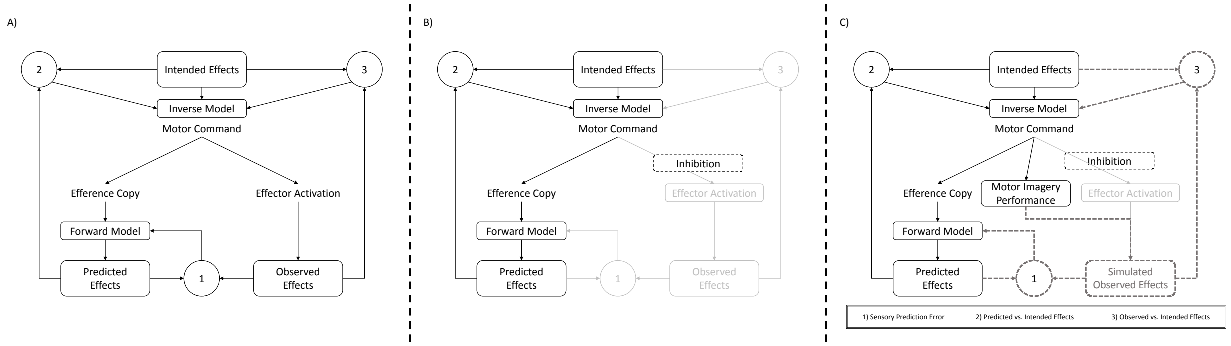

Figure 1. A) Framework for motor learning occurring via overt movement, adapted from Blakemore et al., 2002; briefly, as a motor command is sent to the effectors, the efference copy is used as input to a forward model. The forward model serves to predict the upcoming state of the effectors (predicted effect) and corrects for error (circle 1) by integrating observed effects from the movement. When the movement is completed, the observed and predicted effects of the movement (circles 2 and 3) are compared against the intended effect of movement to minimize the difference between them. B) A proposed framework for motor learning via motor imagery adapted from Dahm and Rieger, 2019; briefly, since movement is not executed in motor imagery, two of three processes used to identify error and correct movement are not utilized in motor imagery, represented by grey lines. Therefore, learning can only occur through comparison of predicted against intended effect (circle 2). C) Theorized changes to the Reiger and Dahm, 2019 model of motor learning in motor imagery to account for the errors in the predicted effects of movement (grey dashed lines). In this model observed effects are simulated via motor imagery performance alongside the predicted effects arising from the forward model enabling comparisons represented by circles 1 (predicted vs. observed effects) and 3 (observed vs. intended effects) to contribute to learning occurring via motor imagery.

Our understanding of motor learning as detailed above arises largely from the study of repeated practice occurring via overt movement. Like overt movement, practice via motor imagery has also been shown to drive motor learning, even independent of overt movement (Ingram et al., 2019; Kim et al., 2017; Ruffino et al., 2021). The basis for the effectiveness of motor imagery for motor learning is grounded in the motor simulation theory, which posits that motor imagery and overt movement are functionally equivalent, in that similar processes occur in the brain when engaging in a motor skill using either modality, with the major difference being that the movement is not actually executed in motor imagery (Jeannerod, 2001). Given that the movement is not actually executed in motor imagery, a paradox is created – if you learn a skill by identifying and correcting errors through the provision of feedback arising from the observed effect of movement (i.e., Fig 1A), how does motor imagery facilitate skill acquisition when the movement is not actually executed? Presumably, such a scenario creates a circumstance where the outcome of the movement is not known, and, as a result, the observed effect of movement cannot be used as feedback to adjust the forward model (Figure 1b; see circle 1). Nor could the observed effect of movement be used as a comparator to the intended effect (Figure 1b; see circle 3) to adjust the motor command for the subsequent trial.

In the scenario outlined above, the only avenue providing a means for error detection and correction would be to use the predicted outcome of movement, generated by the forward model, and compare it against the intended effect of movement (Figure 1B; see circle 2). For learning to occur in this scenario two assumptions need to be true: 1) there must be a mechanism in motor imagery to predict the effect of movement; and 2) this prediction must differ from the intended effect of the planned movement. These assumptions align with the emulation theory of motor imagery, which posits that motor imagery involves a simulation of the movement and its sensory consequences (Grush, 2004). Indeed, emulation theory provides a framework to understand how movement outcomes are predicted in motor imagery. In its simplest form, the emulator uses the efference copy to generate a simulation of the movement and its sensory consequences, akin to a forward model. Until recently however, evidence was lacking to support the notion of forward models in motor imagery. In their elegant study, Kilteni and colleagues provided evidence that forward models are used in motor imagery akin to overt movement (Kilteni et al., 2018). As noted by the authors, when performed via overt movement, the sensation associated with self-touch relative to touch by an external source is attenuated by the forward model's prediction of the tactile feedback (Blakemore et al., 2000). Based on this evidence, Kilteni and colleagues provided tactile feedback to participants as they imagined performance of a self-generated touch, with the tactile feedback serving as a substitute for the sensory input that would result from performing the task overtly. The authors demonstrated that both motor imagery and overt execution of the task resulted in attenuation of the perceived force. The attenuation of the perceived force from the self-generated touch results from the predicted effect of movement, meaning participants must utilize the forward model in both motor imagery and overt movement.

Arising from the finding that integration of forward models in MI is tenable is the question of whether the predicted effects of movement generated in the process of doing motor imagery are simply the motor to sensory transformation of the original motor command (and thus a replicate of the intended effect of movement) or if the predicted effects of movement deviate from this, i.e., do errors result from motor imagery. Results on a dart throwing task whereby participants were to imagine themselves "hitting the bulls-eye" revealed that self-report of the position of their dart on the board after motor imagery performance was inaccurate (Dahm & Rieger, 2019b). This finding demonstrated that motor imagery performance can result in a subjectively experienced error, in line with past work, including that demonstrating the commission of errors in imagined typing (Dahm & Rieger, 2019a). Additionally, the degree of reported error on the task when performed via motor imagery was correlated with error produced in overt execution and was additionally modulated by experience with the task (Dahm & Rieger, 2019b). During performance of a complex motor task, a similar finding was obtained, whereby increasing stimulus complexity and animation velocity negatively impacted both accuracy and self-reported accuracy in the overt execution condition. Likewise, in the motor imagery condition increasing stimulus complexity and animation velocity negatively impacted self-reported accuracy (Ingram, 2021). The observation that motor imagery performance can result in error and that this error is similarly modulated by factors known to affect overt movement supports the theory that movement is simulated in imagery rather than imagery being a predetermined cognitive representation of one's knowledge of the skill and its consequences(Grush, 2004; Pylyshyn, 2002). Additionally, the presence of errors resulting from motor imagery gives rise to the possibility that motor imagery leverages the comparison of the predicted and intended effects of movement to adapt behaviour on subsequent trials to drive motor learning (Figure 1b, see circle 2; Dahm & Rieger, 2019b). However, this finding and the related theory raise an interesting question as to how performance of a movement via motor imagery produces an error.

If one assumes the model outlined in Figure 1B to be correct, the imagination of movement is simply a forward model that does not benefit from the integration of sensory information as the 'movement' progresses, as there would be no observed effect of the movement, as theorized by Dahm and Rieger (Dahm & Rieger, 2019b). In this model, the predicted effect of movement resulting from the forward model would simply be the motor to sensory transformation of the efference copy. As the 'movement' progresses, subsequent comparison of the predicted and intended effect of movement would yield no adaptation over time as the two signals would contain similar information. As evidence indicates motor imagery can drive motor learning, it is more likely that forward models in motor imagery lack precision and thus do not accurately represent the motor commands required to achieve the intended effect, and thus the error arising from the comparison of the predicted to intended effect allows learning to proceed (Figure 1b, circle 3; Dahm & Rieger, 2019b).

While the imprecision of the forward model is a possible explanation of error resulting from motor imagery performance, it ignores the possibility that the observed effects of movement are simulated in the process of imagining a movement (Figure 1c; Grush, 2004; Shadmehr & Krakauer, 2008; Wolpert et al., 2011). According to emulation theory, motor imagery can be represented by a simulation of both the predicted effects of movement as well as the observed effects (Grush, 2004). Should emulation theory be true, the observed effects of movement, simulated in motor imagery, would provide the required input for updating the predicted effects of movement and a comparison against the intended effect of the movement (Figure 1c; see circles 1 and 3 respectively). Here we make a preliminary attempt at testing the theory that the observed effect of movement, simulated in motor imagery, is used in the process of acquiring a novel motor skill.

One approach to testing the plausibility of this theory is to interrupt activity of the brain region thought to be responsible for simulating observed effects in motor imagery (Figure 1c). In overt movement, the process of updating a forward model is attributed predominantly to three regions of the brain: the primary motor cortex, the parietal lobe, and the cerebellum (Desmurget et al., 1999; Popa & Ebner, 2019; Schieber & Poliakov, 1997; Shadmehr & Krakauer, 2008). The primary motor cortex is largely responsible for executing the motor command which gives rise to the efference copy that is used to generate a forward model (Kilteni et al., 2020; Wolpert & Ghahramani, 2000). The parietal lobe integrates the state of the body with sensory information about the surrounding environment and the goal of the movement which is relayed to the cerebellum (Andersen & Buneo, 2002; Block et al., 2013; Caspers et al., 2010; Fogassi & Luppino, 2005; Miall, 2003; Mutha et al., 2011; O'Shea & Moran, 2017). This sensory information is used to form state estimations or representations of the consequences of movement that can then be used to modulate an upcoming or ongoing motor plan realized by reciprocal cerebro-cerebellar connections or a recently identified sensory-parietal-motor loop (Blakemore & Sirigu, 2003; Medendorp & Heed, 2019; Pilacinski et al., 2018; Richard et al., 2021). The cerebellum is thought to be responsible for housing and updating the forward model (Miall et al., 1993; Miall & Wolpert, 1996). Based on the role of the parietal lobe in integrating proprioceptive and environmental information for movement, its consistent activation during the performance of movement via motor imagery and the inability of patients to perform motor imagery when the parietal lobes are damaged, we theorized that the parietal lobe was a likely candidate brain region that contributes to or is the source of the simulated observed effects of movement in motor imagery (Figure 1c; Burianová et al., 2013; Hardwick et al., 2018; Hétu et al., 2013; McInnes et al., 2016; Sirigu et al., 1996). In addition to the above, past work has demonstrated that inhibitory brain stimulation delivered to the left inferior parietal lobe (L_IPL) prior to practice occurring via motor imagery abolishes motor imagery-based learning, demonstrating the region's importance to skill acquisition via motor imagery (Kraeutner et al., 2016). However, given that the inhibitory stimulation was delivered prior to the motor imagery-based practice and its inhibitory effect persisted throughout the experiment, it was not possible to identify the L_IPL’s potential role in the process of motor imagery-based motor learning (Figure 1c). Said another way, this finding only highlights that the L_IPL is important to motor imagery-based learning but does not permit insight into its possible role in integrating simulated movement outcomes during motor imagery performance. To gain insight into the role of the L_IPL in motor imagery-based motor learning, single pulse TMS applied at an appropriate time could be used to selectively interfere with the function of the area.

Given the need for greater temporal specificity in the inhibition of the L_IPL, here we used single-pulse transcranial magnetic stimulation (TMS) delivered shortly after each trial of task practice via motor imagery to transiently inhibit the L_IPL. This paradigm specifically probes the L_IPL’s involvement in providing the simulation of the observed effects of the movement during motor imagery as a metric for comparison against the intended effect of movement (Figure 1c; see circle 3). In the first of two sessions, participants engaged in the execution of kinematic trajectories of varying complexity via motor imagery for four blocks of 20 trials followed by a single block of 20 trials that were performed overtly to assess performance. The second session comprised a retention test that was identical to the final block of session one. Participants were randomly assigned to one of two groups who received either non-invasive inhibitory TMS to the L_IPL (‘stim’) or over the vertex of the head (‘sham’) 100ms after each trial. This approach has been shown to transiently alter neural processing in the region receiving the stimulation, and thus for the current experimental paradigm, the stimulation would interfere with the integration of the simulated observed effects required to draw a comparison against the intended effect of movement, contributing to motor learning (Figure 1c; see circle 3; Prime et al., 2008). Specifically, we hypothesized that inhibitory single pulse TMS to the L_IPL would impair learning relative to the group receiving stimulation over the vertex of the head.

METHODOLOGY:

Participants. Forty-three participants with normal or corrected to normal hearing and vision, no history of neurological injury, and who reported no contraindications to TMS were recruited for the study. Of the 43 participants recruited, one withdrew from the study during the first session and 8 were lost to technical errors leaving a final sample of 35 participants. Participants were aged 22.4 ± 3.5 (mean±S.D.) years with 22 identifying as female and 13 as male. Handedness was determined via the Edinburgh Handedness Inventory (Oldfield, 1971) and ability to perform motor imagery assessed using the Kinesthetic and Visual Imagery Questionnaire (KVIQ; Malouin et al., 2007). Most participants were right hand dominant (n=30) with the remaining left hand dominant (n=4) or ambidextrous (n=1). Participants were randomly assigned to one of two groups: ‘sham’ or ‘stim’ (see Transcranial Magnetic Stimulation below). The stim (n=17) and sham (n=18) groups were balanced across sex (11 and 6; 11 and 7 for female and male for the stim and sham groups respectively) age (22.5 ± 3.1 and 22.2±3.9 years for the stim and sham groups respectively) and imagery ability in the kinesthetic domain (KVIQ kinesthetic scores: 20.8 ± 3.4 and 21.5 ± 3.1 for the stim and sham groups respectfully). Each participant provided written informed consent and were oriented to the task by the investigator. Ethical approval was obtained from the Dalhousie University health sciences research ethics board.

Task Description. We used a motor task that required repeated execution of kinematic trajectories of varying complexity, for which learning has been previously demonstrated using both overt movement and motor imagery (Ingram et al., 2019); https://github.com/LBRF/TraceLab). Trials consisted of animation of a complex trajectory on a touchscreen followed by the participants response. Stimuli consisted of either randomly generated trajectories or a repeated trajectory, the latter which was to be learned. Learning is determined by comparing the magnitude of error on repeated relative to random trajectories. For the present study, the original paradigm was reduced in total trial number from 500 to 120 and compressed into two study sessions (training/testing in session one and a retention test in session two; Figure 2). Given this change, we confirmed via pilot testing participants ability to learn the repeated trajectory in a single session. To accommodate the delivery of TMS, the original code was modified to integrate control of the TMS system using the MagPy package in Python (McNair, 2017). A complete description of the task is reported in Ingram et. al. 2019. Briefly, participants were seated upright with their chin positioned in a chin rest to both minimize muscle fatigue and head movement during task performance and to facilitate accurate localization of the TMS. A 24” touch screen monitor with 1080p resolution and 60Hz refresh rate (Planar Helium PCT2485) was located approximately 12” in front of the participant, lying flat on a table. This orientation of the touchscreen allowed for unobstructed viewing and for the participant to comfortably reach the screen (Figure 3).

Trial Description. Stimuli were animated trajectories that consisted of 5 connected Bezier curves. Trajectories started at the midline of the lower half of the touchscreen, with animation proceeding in a clockwise direction where Bezier curves connected 4 control points (one in each quadrant of the screen) before returning to the start point. As above, stimuli consisted of random trajectories that were generated at the beginning of each trial and a repeated trajectory that was generated at the outset of the first study session and remained consistent for each participant throughout. Trajectory complexity, measured as the sum of the interior turn angles, inherently varies as a function of the random trajectory generation, indicating that random shapes would not likely be equally as complex as the repeated trajectory. To ensure the random and repeated trajectories were of similar difficulty, the repeated trajectory used in this experiment was chosen from the set of repeated trajectories utilized in Ingram et al. 2019, which were selected based on their similarity to the mean complexity of random trajectories generated in this paradigm. Stimuli were presented at a 1:1 (random to repeated) ratio and trials were animated at 5 different durations (500, 1000, 1500, 2000, and 2500ms) such that there was equal exposure across stimulus type and animation durations. In session one, participants performed 5 blocks of 20 trials, with each block equally divided between random trajectories and the repeated trajectory pseudo randomly presented at each animation duration, resulting in the presentation of 50 trials each of random and the repeated trajectory distributed evenly across animation durations. In session two, participants performed one block of 20 trials equally divided between random and the repeated trajectory distributed evenly across animation durations (Figure 1a).

Participant responses were made using either imagined or overt movement: in session one, blocks 1-4 were considered training blocks during which participants responded using motor imagery, while block 5 was considered a testing block, requiring participants to respond using overt movement to allow performance to be assessed. In session two, participants responded using overt movement exclusively. Regardless of response modality, a trial began with the participant lifting their index finger from a position in the lower right corner of the touchscreen, at which point the participant observed a white dot animating the stimulus (i.e., the trajectory) beginning at the start point. After the presentation of the stimulus, a red circle appeared at the start / end point of the trajectory. For motor imagery trials, the participant placed their index finger on the red circle, at which point it turned green, prompting the participant to imagine themselves performing the movement (i.e., completing the trajectory). When they had completed the imagination of the movement, participants lifted their finger off the screen, ending the trial. If participants moved their arm during the trial (i.e., overtly performed the task), a mistrial resulted when their finger left the green circle. Trials involving overt movement proceeded in the same manner as that of the motor imagery trials, with the exception that participants performed the movement. For all trials, participants responded with their dominant hand and were asked to match the speed at which the stimulus was presented to the best of their ability.

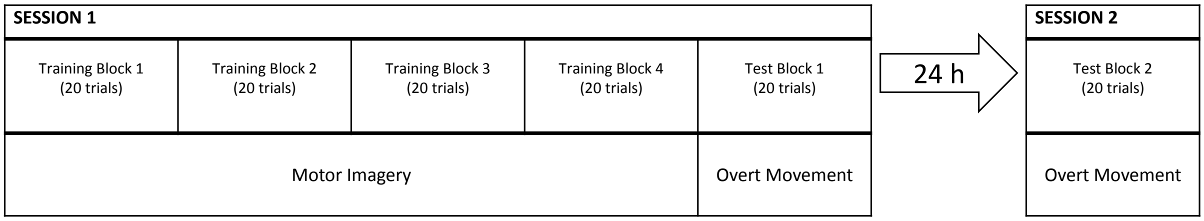

Figure 2. Experimental timeline. Following informed consent, screening and questionnaires, participants completed 4 blocks of training via motor imagery, receiving TMS 100ms after each trial to the L_IPL (stim group) or over the vertex of the head (sham group), followed by a test block of 20 trials performed overtly (Test Block 1). The second session consisted of an identical test block to assess learning of the task (Test Block 2). The ratio of repeated to randomly generated trajectories in all blocks was 1:1.

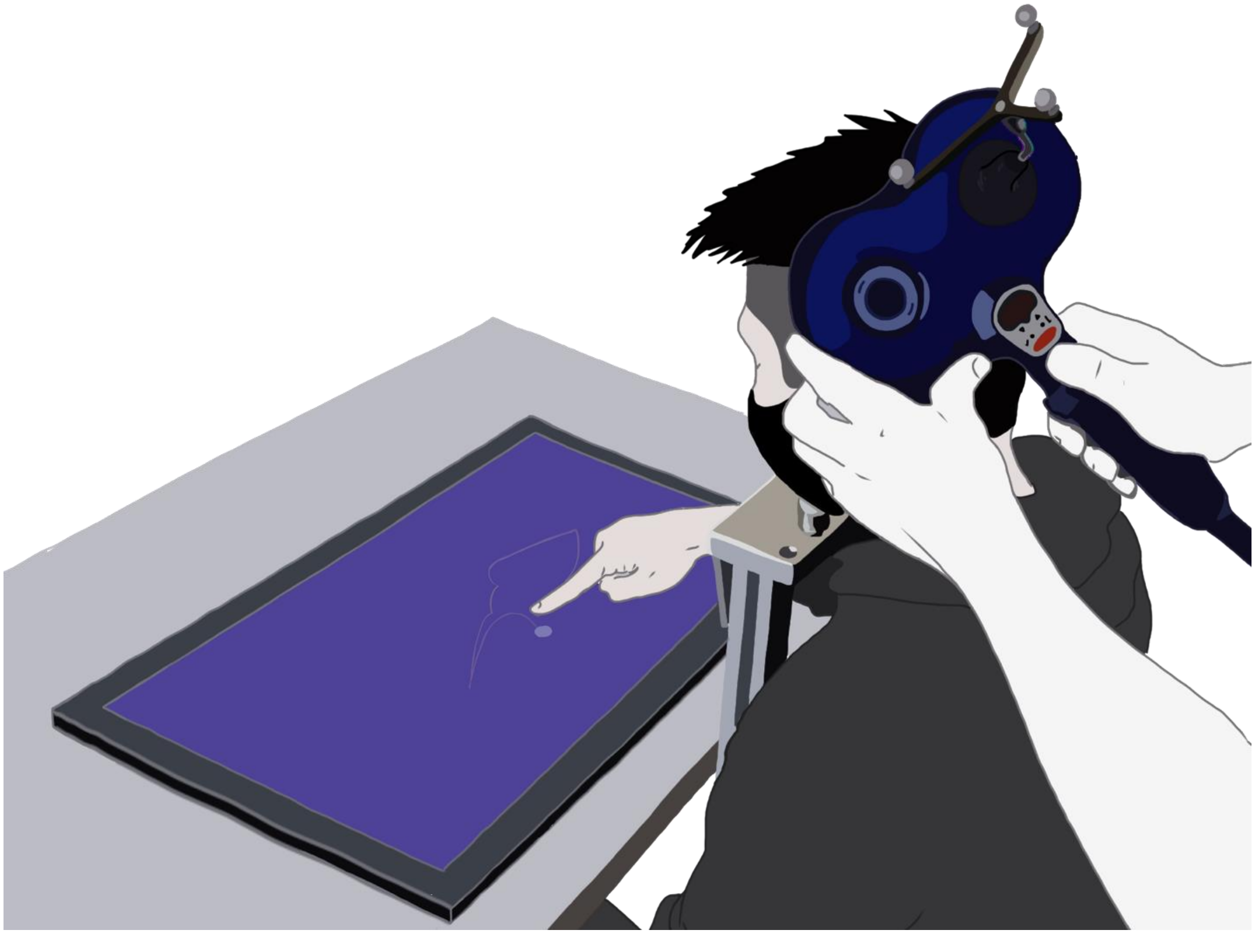

Figure 3. Experimental set-up. Participants reproduced complex trajectories via motor imagery (practice trials) and overt movement (assessment) on a touchscreen monitor. Inhibitory brain stimulation was delivered via transcranial magnetic stimulation over the L_IPL (stim group only). Overt movement trial shown to demonstrate an example trajectory. Note: trajectory shown for illustrative purposes only; feedback was not provided to participants during overt movement trials.

Transcranial Magnetic Stimulation. Neuro-navigated TMS was performed using a BiStim^2 magnetic stimulator via a 70-mm figure of eight coil (Magstim, Whitland, UK) coupled with a Brainsight^{TM} system (Rogue Research Inc., Montreal, Canada). For neuro-navigation, each participant's head was co-registered to a template MRI (MNI152_T1_1mm) by digitizing three anatomical landmarks (left and right pre-auricular points and the nasion). Consistent with prior work showing effective inhibition of the IPL, an online inhibitory TMS protocol in which single pulses of TMS were delivered to the left IPL (-36, -23, 34 [X, Y, Z]; MNI space; Kraeutner et al., 2016) at 60% of stimulator output (stim group; Prime et al., 2008) was used. In the sham group, TMS was delivered to a point over the vertex of the head at 15% of stimulator output. Single pulses were delivered with the coil held tangentially to the participants scalp at a 45° angle to the anterior-posterior axis (Figure 3), with the stimulation delivered 100ms after the conclusion of each trial (i.e., after the participant lifted their finger from the touchscreen). The timing of the TMS pulses was controlled by the MagPy package in Python; this approach ensured that the TMS pulse was consistently delivered 100ms post trial completion despite the varied length of each trial (McNair, 2017).

Experimental Protocol. At the onset of the first study session, participants were familiarized to kinesthetic motor imagery by a video that described this type of imagery and explained how to perform the task via motor imagery. Kinesthetic motor imagery was used as it better facilitates motor skill learning relative to visual motor imagery (Stinear et al., 2006). Handedness was then determined, and participants completed the KVIQ. Participants then completed the 5 blocks of the experimental task. Approximately 24h later, participants returned to the laboratory to complete a single block of the experimental task which comprised the retention test. A detailed timeline is shown in Figure 2.

Data Analysis. Analysis procedures were based on those of Ingram et al. 2019 apart from additional filtering processes to remove noise introduced through various errors identified during visual inspection as part of preliminary data analysis. These errors included: spurious data samples from the touchscreen (i.e., touchscreen recording a sample in a random location on the screen); multiple contact points (i.e., when a participant's wrist and finger(s) contacted the screen at the same time); false starts (i.e., participant having difficulty initiating a trial); and missed endpoints (i.e., participant failing to return to the endpoint at the end of the trial). These errors were handled via additional filtering (https://github.com/LBRF/TraceLabAnalysis) which removed the corresponding data points from the raw data and then interpolated the missing data points. In instances where the gap in samples due to data being removed exceeded a threshold related to time, distance, or distance and angle, then the trial was removed from further analysis. Trials were removed from the analysis if the time gap between any samples in the participant response mid trajectory was longer than 170ms (indicating that at least 10 consecutive samples were removed) or if the distance between the last sample prior to the gap and the first sample after the gap exceeded 500 pixels. When the gaps in data in the participant's response occurred at the same time as a 'corner' in the stimulus, the time and distance filters were more restrictive. This filter was multilevel to identify gaps where a participant sharply changed direction over a small distance (e.g., a change of direction >90° over a distance <180 pixels) or when a participant made a more gradual change in direction over a longer distance (e.g., a change of direction >120° over a distance >250 pixels). If trials met either of these criteria they were removed from the analysis. Trials where a participant's response time exceeded > 2 sec of the stimuli animation duration were also removed from the analysis. The variability in participant's response speed with reference to the presented stimuli in the remaining trials were handled using dynamic time warping. The error metric for the trajectory was operationalized as the mean Euclidean distance (pixels) between consecutive samples from the stimulus trajectory and the participant's response trajectories after each of these processes were applied to the data. In addition to the calculation of the error metric for each trajectory, the stimulus's animation velocity was calculated for each trial by dividing the total trajectory length (px) by the duration of time needed to animate the trajectory.

Statistical Analysis. Bayesian linear mixed-effects regressions were used to make statistical inferences regarding group performance on the task across study sessions. All models were run using the "brms" package for R (version 3.6.3). To ensure that participants were attending to the task, a model was used to predict participants movement time. The duration of the participants' responses was predicted by the stimulus duration (ms) and modality (motor imagery or overt movement) while controlling for random participant effects (random intercept for participant) and the effects of movement time and modality within participants (random slopes of participant | movement time X modality). The final model used fixed effects of trial type (random or repeated), session (1 or 2), group (sham or stim), animation velocity (total trajectory length/stimulus duration; px/s), and trajectory complexity (turn angle sum) to predict error (px) while controlling for participant performance (random intercept for participant) and the effects of animation velocity, trial type and session within participants (random slopes of participant | animation velocity X trial type X session). If the maximum probability of effect (MPE) was >90% for any fixed effect, then the effect was deemed credible and was selected for post hoc analyses via the 90% highest probability density intervals (HPDI). For effects that were near the 90% MPE, the proportion of the posterior distribution for that effect in the region of practical equivalence (ROPE percentage) was additionally interpreted to determine if the effect was real. Visualizations and post-hoc comparisons were created by using draws from the posterior probability distribution of the model, holding various predictors constant to isolate effects of interest. Values presented for the descriptive measures are mean ± standard deviation throughout.

Transparency and Openness. All data, analysis code, and research materials are available by emailing the corresponding author. Data were analyzed using R, version 3.6.3 (R Core Team, 2020) and the packages *tidyverse* version 1.3.1 (Wickham, 2014), *vegan 2.5-7*, *TSEntropies 0.9*, *bmrs 2.16.1*, tidybayes 3.0.1, *parameters 0.14.0* and *emmeans 1.6.3*. This study's design and its analysis were not pre-registered.

RESULTS:

Movement time. After controlling for within participant effects on each stimulus duration, statistical testing revealed credible main effects of modality and stimulus duration and an interaction between modality and stimulus duration at the 1000ms level of stimulus duration. The main effect of stimulus duration revealed that participants modulated the length of their movements in response to the increasing length of the stimulus (1000[MPE = 1, 90% HPDI: 0.62 to 0.48, ROPE Percentage = 0], 1500[MPE = 1, 90% HPDI: 0.98 to 0.82, ROPE Percentage = 0], 2000[MPE = 1, 90% HPDI: 1.32 to 1.16, ROPE Percentage = 0] and 2500[MPE = 1, 90% HPDI: 1.56 to 1.38, ROPE Percentage = 0], all comparisons against the 500ms level, Figure 4). Participants were consistently slower during motor imagery in comparison to overt movement, a finding consistent with previous results using this paradigm (MPE = 0.96, 90% HPDI: -0.01 to -0.36, ROPE Percentage = 0.21, Figure 4; Ingram et al., 2019). There was also an interaction effect, whereby at the 1000ms duration motor imagery was slower than overt movement by a larger margin than reported at other levels (MPE = 0.96, 90% HPDI: -0.02 to -0.25, ROPE Percentage = 0.34, Figure 4).

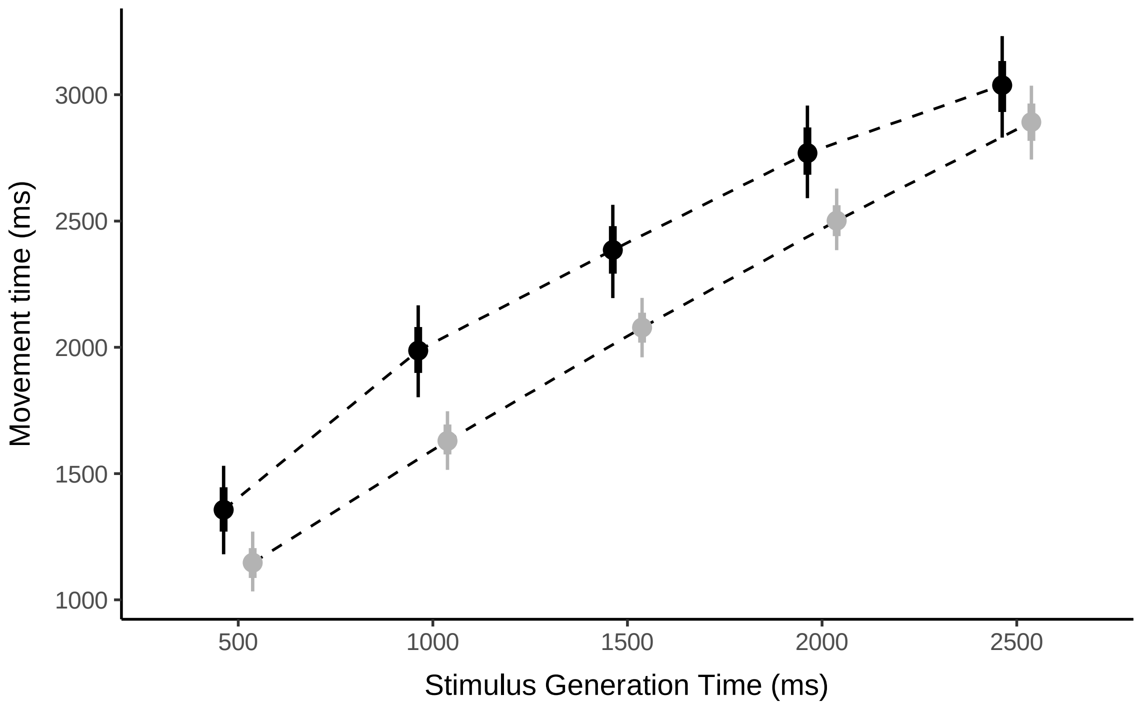

Figure 4. Scatter plot of participants' movement times at different stimulus durations in each modality (black: motor imagery; grey: overt movement) after controlling for within participant effects. Thick vertical bars indicate 60% HDPIs and thin vertical bars indicate 90% HPDIs.

Error. Error on the random and repeated trajectories in the sham group was 96.0±38.2px and 92.2±26.4px in session one and 101.6±47.4px and 91.4±25.4px in session two. For the stim group, error on the random and repeated trajectories was 96.1±32.3px and 89.8±21.5px in session one and 100.3±39.0px and 88.5±24.5px in session two (Table 2, Figure 5a). After controlling for the effects of trajectory complexity and animation velocity the mean error for participants in the sham group in session one was estimated from the model's posterior distribution to be 94.7±7.2px and 85.4±6.2px (mean ± 90% HPDI) and 95.6±9.2px and 85.8±8.0px (for random and repeated trajectories respectively) in session two. In the stim group, the mean error on random and repeated trajectories were estimated to be 93.6±7.0px and 84.6±6.5px in session one and 94.1±9.4px and 85.1±7.8px in session two (Table 2, Figure 5b).

Table 2. Mean trajectory error calculated from the observations (mean ± SD) and drawn from the posterior distribution of the Bayesian model, and error controlling for animation velocity and trajectory complexity (mean±90% HDPI) for each group separated by trial type.

Group	**Trial type**	**Raw Error (mean ± SD)**		**Controlled Error (mean ± 90% HPDI)**	
		Session 1	Session 2	Session 1	Session 2
Sham	Random	96.0±38.2px	101.6±47.4px	94.7±7.2px	95.6±9.2px
	Repeated	92.2±26.4px	91.4±25.4px	85.4±6.2px	85.8±8.0px
Stim	Random	96.1±32.3px	100.3±39.0px	93.6±7.0px	94.1±9.4px
	Repeated	89.8±21.5px	88.5±24.5px	84.6±6.5px	85.1±7.8px

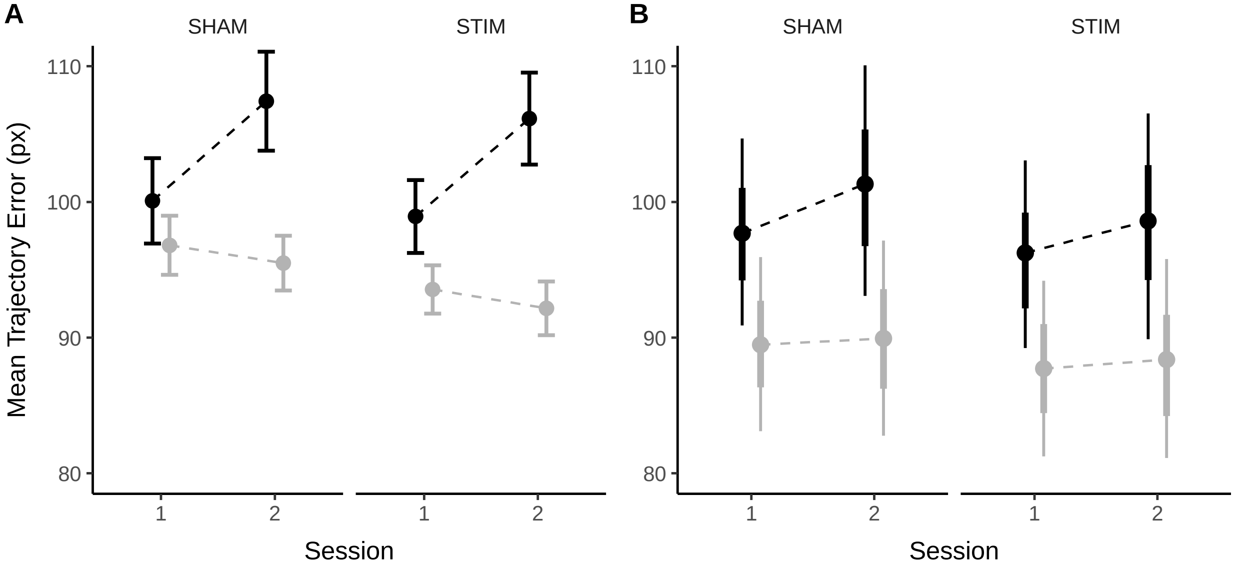

Figure 5. A) Scatter plot of the effects of figure type (black: random; grey: repeated) within the Sham and Stim groups across both experimental sessions on raw error. Vertical bars indicate standard error. B) Scatter plot of the effects of figure type (black: random; grey: repeated) within the Sham and Stim groups across both experimental sessions on trajectory error after controlling for the effects of animation velocity and complexity. Thick vertical bars indicate 60% HDPIs and thin vertical bars indicate 90% HPDIs.

The model highlighted several highly credible main effects including trial type, animation velocity and trajectory complexity (Figure 6a-c), five separate two-way interactions (trial type X animation velocity, session X trajectory complexity, session X trial type, session X animation velocity, animation velocity X trajectory complexity) and a three-way interaction (group X animation velocity X trajectory complexity). The main effect of trial type demonstrates that participants performed better on the repeated trajectory than on the randomly generated trajectories (MPE = ~1, 90% HPDI: 0.20 to 0.12, ROPE Percentage = $5.0X10^{-5}$, Figure 6a). The effects of both animation velocity and trajectory complexity indicate that participants had a greater difficultly producing the stimulus trajectories as the stimulus animation velocity increases (MPE: ~1, 90% HPDI: 0.65 to 0.46, ROPE Percentage = 0, Figure 6b) and as the stimulus becomes increasingly complex (MPE: ~1, 90% HPDI: 0.21 to 0.06, ROPE Percentage = 0.19, Figure 6c). All of the posterior distributions for the credible two- and three-way interactions were mostly contained within the region of practical equivalence (>50% within the ROPE) and were not interpreted: 1) trial type X animation velocity (MPE= 0.96, 90% HPDI: 0.15 to $7.34X10^{-3}$, ROPE Percentage = 0.67), 2) session X trajectory complexity (MPE= 0.96, 90% HPDI: 0.15 to $3.38X10^{-3}$, ROPE Percentage = 0.71), 3) session X trial type (MPE= 0.92, 90% HPDI: 0.01 to -0.11, ROPE Percentage = 0.93), 4) session X animation velocity (MPE= 0.90, 90% HPDI: 0.02 to -0.13, ROPE Percentage = 0.82), 5) animation velocity X trajectory complexity (MPE= 0.92, 90% HPDI: 0.13 to -0.15, ROPE Percentage = 0.72) and 6) group X animation velocity X trajectory complexity (MPE= 0.97, 90% HPDI: 3.81X10^{-3} to -0.17, ROPE Percentage = 0.58).

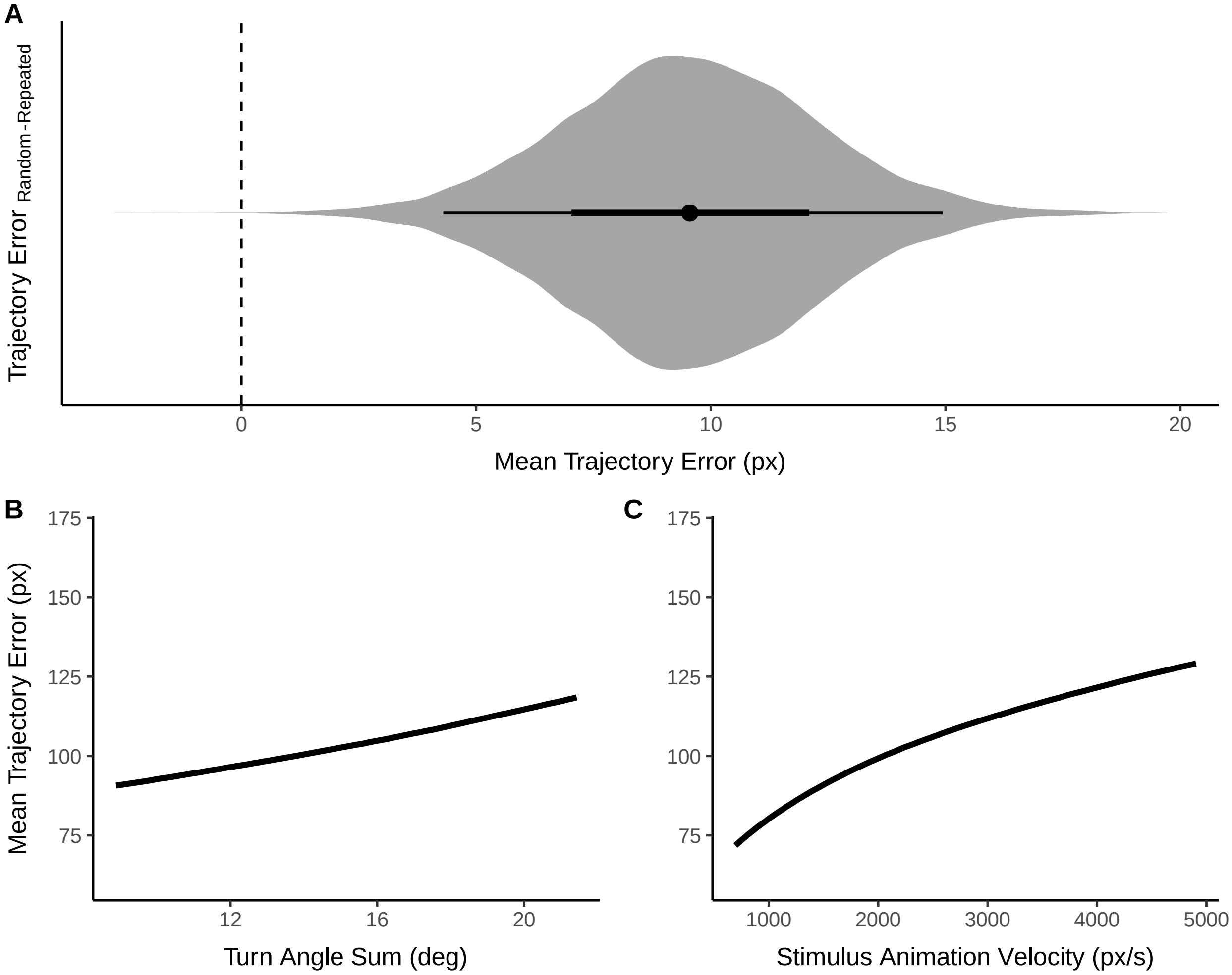

Figure 6. A) The distribution (grey shaded area) of differences between trajectory error on random and repeated trajectories controlling for all other predictor variables. The thick horizontal bar indicates 60% HDPIs and thin horizontal bar indicates 90% HPDIs. B) The effect of animation velocity on trajectory error controlling for all other predictor variables. The grey

shaded area represents the 90% HDPI. C) The effect of trajectory complexity on trajectory error controlling for all other predictor variables. The grey shaded area represents the 90% HDPI.

The model also revealed two higher order interactions between session, group, trial type, animation velocity and trajectory complexity that were moderately or weakly credible but were narrowly above or below our threshold for credible findings (MPE >90%). Like the credible interaction effects, the posterior distribution of the HPDI for these effects were largely contained within the region of practical equivalence and as such were not interpreted. These higher order interactions included session X trial type X animation velocity (MPE= 0.88, 90% HPDI: 0.02 to -0.13, ROPE Percentage = 0.86) and group X session X trajectory complexity (MPE= 0.83, 90% HPDI: 0.03 to -0.11, ROPE Percentage = 0.91).

DISCUSSION:

The purpose of this study was to determine if the observed effect of movement, simulated in motor imagery, is used in the process of acquiring a novel motor skill. Given prior evidence, we postulated that the L_IPL is a reasonable candidate region responsible for the generation of the simulated observed effects of movement required to permit comparison against the intended effect of movement (Figure 1c, see circle 3). To investigate this query, participants received inhibitory TMS 100ms after each trial at either 60% of stimulator output to their L_IPL or 15% of stimulator output over the vertex of the head while repeatedly executing kinematic trajectories via motor imagery. Learning on the task was assessed immediately after training and on a subsequent day by comparing participant’s performance on a trajectory that was continually presented to the participant during training (the repeated trajectory) to trajectories that were randomly generated. The more accurate a participant was at producing the repeated trajectory in comparison to random ones indicated the degree of learning. We confirmed adherence to the task as the main effect of stimulus duration indicates that movement time in both motor imagery and overt execution scaled as a function of increasing stimulus duration. Both conditions were slowed in comparison to stimulus duration as the path length of the random stimuli were not controlled and some shapes were too long to be drawn in the appropriate time consistent with pervious findings (Ingram et al., 2019). The main effect of trial type indicates participants learned the task, a finding consistent with our prior work. We attributed the change in performance observed here to motor imagery-based learning as our prior work demonstrated the magnitude of learning via motor imagery was greater than that observed for a perceptual (control) condition (Ingram et al., 2019). Consistent with motor learning literature, factors which varied task difficulty in the present study, animation velocity and trajectory complexity, impacted participant performance as increasing either resulted in greater mean error.

Our a priori hypothesis stated that TMS delivered to the L_IPL would interfere with learning on this task as represented by a significant interaction between group and trial type. However, the null hypothesis was not rejected as these two factors did not significantly interact. Three plausible explanations exist to explain this null finding. Firstly, it could be concluded that the model for motor learning occurring via motor imagery is as reported by Dahm and Rieger, whereby only the comparison of predicted and intended effects drives motor learning (Figure 1b). Secondly, the L_IPL is not involved in the process of generating simulated observed effects of movement for comparison against its intended effect (Figure 1c, see circle 3). Finally, there could be incongruency between the proposed function of the L_IPL and the timing of the stimulation that was intended to interrupt it.

Since movement is not performed in motor imagery it is still possible that solely using the forward model to predict the effect of movement is the method in which motor imagery drives learning (Dahm & Rieger, 2019b). In this framework, the predicted effects of movement generated from the forward model would not be altered in real time by simulated observed effects of movement and thus ultimately would be an unaltered motor-to-sensory transformation of the efference copy. Since it has been demonstrated that motor imagery can result in the prediction of errors, the motor plan representing the movement would inherently need to contain an error as there is no avenue to modify the predicted outcome of the movement once the forward model is created (Dahm & Rieger, 2019b). We think that this explanation is unlikely; alternatively, a more plausible explanation is that the observed effects of movement are simulated alongside the predicted effects of movement, as suggested by the emulation theory of motor imagery. The process detailed in emulation theory provides a means for the forward model to be altered when a movement is 'performed' via motor imagery. Essentially, a participant initiates the motor plan and errors arise as the movement is 'performed' via motor imagery (see introduction for elaboration on this idea). A key question then is what part of the brain is responsible for the simulated observed effects of movement in motor imagery.

The null finding observed would suggest the L_IPL is not involved in generating the simulated observed effects of movement required to make a comparison against the intended effect of movement. Based on its role in adjusting forward models during overt movement, another candidate region to be involved in this process would be the cerebellum (Miall, 2003; Popa & Ebner, 2019; Shadmehr & Krakauer, 2008). The cerebellum can influence activity of the motor cortex via the dentatothalamocortical pathway and has been reported as being active during MI performance, although to a lesser degree than during overt movement (Burianová et al., 2013; Hardwick et al., 2018; Horne & Butler, 1995). Recent evidence has suggested that the cerebellum can inhibit areas in the sensorimotor cortex and may be responsible for limiting the output from the contralateral motor cortex in motor imagery (Cengiz & Boran, 2016). In the context of learning, the cerebellum is thought to be responsible for online movement control by interpreting proprioceptive feedback about the movement and location of the effector to update the forward model (Shadmehr et al., 2010). However, in motor imagery, it is possible that the IPL does not provide proprioceptive information to the cerebellum as the movement is not performed, and the forward model is updated absent that input (Figure 1c, circle 1). That the cerebellum may update the forward model absent input from sensory association regions gives rise to a proposed mechanism in which learning in motor imagery is driven exclusively by the cerebellum (Galea et al., 2011; Wolpert et al., 1998). Future research could probe this potential mechanism in motor-imagery based learning by inhibiting the cerebellum using either a battery of conditions providing transient inhibition at different timepoints during motor imagery performance or using inhibitory TMS protocols (e.g., continuous theta burst stimulation).

Despite this study’s null finding, the literature has demonstrated that the IPL is vital for motor imagery-based performance and learning. Given the role of the IPL in integrating sensory information with the goal of movement, it’s dense connections with frontal regions of the brain including the premotor cortices, it’s consistent activation during motor imagery and the noted modulation of activity in the L_IPL over the course of learning new motor skills, we postulated that this region is vital for the simulation of movement during MI (Andersen & Buneo, 2002; Fogassi et al., 2005; Fogassi & Luppino, 2005; Hardwick et al., 2018; Hétu et al., 2013; Ruffino et al., 2017). The importance of the L_IPL and its potential role in simulating movement and its outcome is further reinforced by impairment in the ability to perform motor imagery or learn via motor imagery in participants that have damage to the left parietal lobe or were subject to the effects of repetitive TMS causing inhibition of that region (Kraeutner et al., 2016; McInnes et al., 2016). However, the limitation of the study of patients with damage to the parietal lobe or participants subjected to repetitive TMS is that while the overall importance of the damaged or inhibited brain region to a task or process can be assessed, its specific role is difficult to assess given the blanket nature of the disruption of activity. An approach such as single-pulse TMS permits more targeted assessment of a regions specific role as it allows temporal specificity in relation to the process being probed. For instance, in reaching tasks, single-pulse TMS to the IPL 250ms after the presentation of a movement goal and prior to the corresponding reaching action has been shown to impair the representation of a reach vector by disrupting the estimation of the initial hand position (Vesia et al., 2008). Similarly, in mental rotation tasks short trains of TMS applied 400-600ms post stimulus presentation also negatively impacted participant performance (Harris & Miniussi, 2003). From this (and other) research, it is evident the timing of the stimulation to the IPL will impact on whether the process being probed is disrupted or not, and ultimately then on our ability to make inferences about the role of the IPL in said process. In the present study, the primary limitation was the timing of the single-pulse TMS. It is possible that the chosen time of stimulation, 100ms after the conclusion of movement, may not align with the provision of the simulated observed effects of movement to the subsequent comparators (Figure 1c, circles 1 and 3). Small differences in the timing of application of TMS can have significant effects on the observed behaviour; Mars et al. 2009 showed that 50ms changes in the timing of stimulation applied to the pre-SMA caused significant changes in the size of a subsequent motor evoked potential, highlighting the importance of the timing of TMS in probing the proposed function of a brain region (Mars et al., 2009). It could be that the L_IPL is only active during the imagination of the movement (i.e., motor imagery performance) and as such providing the inhibitory stimulation 100 ms after the conclusion of the movement did not disrupt this role. Given this, the conclusion of the study is more accurately stated as the L_IPL is not involved in the provision of the simulated observed effects of movement for comparison against the movement's intended effects 100ms post motor imagery performance (Figure 1c, circle 3). Future research could vary the timing of the single-pulse TMS applied in this task to confirm or refute the role of the L_IPL in simulating the observed effects of movement in motor imagery. Finally, it is important to note that the stimulator output was fixed for all participants. This approach is consistent with prior work contending that the use of motor threshold for determining individual stimulus intensity in non-motor areas of the brain may not be appropriate. (Prime et al., 2008). With that said, it is possible this approach resulted in variability in the TMS-induced electrical field and in-turn an inconsistent dose of TMS across participants.

CONCLUSION:

The present study sought to investigate if the L_IPL was involved in the process of simulating the observed effects of movement for comparison against the movement's intended effects in motor imagery-based learning through transient inhibition of the region after each trial performed via motor imagery. Results of the study failed to reject the null hypothesis as the inhibition of the L-IPL did not impair learning of the task. As such, it was concluded that either the L_IPL is not involved in simulating the observed effects of movement in motor imagery, or the timing of the simulation was incongruent with the theorized role of the L_IPL in motor imagery-based motor learning.

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