# Imagined movement accuracy is strongly associated with drivers of overt movement error and weakly associated with imagery vividness

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Analysis code and those related to the experimental task are openly available online (https://github.com/LBRF/DEMI_Analysis_Pipeline and https://github.com/LBRF/TraceLab). Data is available upon request to the corresponding author. The study was not pre -registered.

We have no known conflict of interest to disclose.

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## Abstract

Theories of motor imagery conflict in their account of what happens during an imagined movement, with some suggesting that movement is simulated while others suggest it involves creating and elaborating upon an internal representation of the movement. Here we report evidence that imagery involves the simulation of a movement and that it varies in accuracy. Two groups of participants performed a motor task focused on challenging movement execution either overtly or via motor imagery. Overt performance was used to model expected performance given required movement characteristics (i.e., speed, complexity, familiarity), which was then compared with self-reported accuracy during imagery. Movement characteristics had a large effect on self-reported accuracy compared to a small effect of imagery vividness. Self-reported accuracy improved across trials with familiar movements compared to novel movements in a similar manner for each group. The complexity of the imagined movement did not influence movement time during imagery or overt trials, further suggesting that imagined movements are simulated rather than abstractly represented. Our results therefore support models of motor imagery that involve the simulation of a movement and its viability, which may be the basis of imagery-based motor learning.


**Public significance statements**

- The commission of errors, necessary for learning new movements, occurs when movements are imagined, a process called motor imagery
- Like what occurs when one actually performs a movement, error increases based on the speed of performance or the complexity of the task when the task is imagined
- Results support the use of motor imagery for learning new movements

Keywords: accuracy; error; execution; motor imagery; motor learning

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Motor imagery and its relationship with overt movement and motor learning remains an active area of debate (Glover & Baran, 2017; Hardwick et al., 2018; O'Shea & Moran, 2017). Interest in motor imagery is driven to a large degree by its potential applications — particularly as a modality to drive motor learning and in-turn recovery in neurological rehabilitation (Barclay et al., 2020; Braun et al., 2008; Silva et al., 2020; Stockley et al., 2021). It is therefore critical to understand the mechanisms of imagery-based motor learning, which is typically investigated by comparing imagery to overt movement.

Theories of motor imagery posit varying levels of similarity between imagery and overt movement. The highly influential motor simulation theory asserts that motor imagery is the experience of covert action that parallels movement planning and in some interpretations movement execution, giving rise to the notion of functional equivalence, such that aside from the absence of movement, motor imagery involves the same computational and neurophysiological processes as overt movement (Decety, 1996; Jeannerod, 1994; O'Shea & Moran, 2017). While sharing some theoretical construct with motor simulation theory related to the simulation of overt movement, motor emulation theory proposes an emulation process that involves the simulation of movement and its sensory consequences (Grush, 2004). Competing theories propose that motor imagery is largely an abstract cognitive process that does not recruit the motor system (Annett, 1995). More recently authors propose a middle ground whereby motor imagery shares in some processing involved in overt movement, such as motor planning, but then diverge into an entirely different process when the movement reaches the execution stage (Glover & Baran, 2017). Depending on experimental details, behavioural and neuroimaging studies provide limited support for any one of these perspectives. That is, motor imagery and overt movement share activation patterns in some brain regions, but also show differences in others (Glover et al., 2020; Hardwick et al., 2018; Hetu et al., 2013). Thus, it remains unclear how imagery may be used to drive motor learning in a way that derives similar benefits as practicing via overt movement.

The variety of results reported in the literature may be explained by the wide range of tasks used. Several potential processes may be differentially recruited depending on the demands of the experimental task. Overt movement is understood as involving several interdependent processes, such as perceptual processing, goal selection, decision making, motor planning, action selection and finally execution (Verwey et al., 2015; Wong et al., 2015). Improvements in performance — and over time, learning (Kantak & Winstein, 2012) — can be attributed to changes in any combination of these processes. For instance, one may learn to better recognize patterns that shape task demands (Wilson et al., 2010), create or refine a motor plan (Wong et al., 2016), or improve the quality of movement execution (Shmuelof et al., 2012). Experimental tasks such as serial reaction time (SRT) tasks likely bias the participant to rely on perceptual or cognitive rather than motor processes (Ingram et al., 2016; Shmuelof et al., 2012; Wong & Krakauer, 2019). Few motor imagery studies employ tasks that challenge motor execution and assess performance changes via the speed-accuracy function (Ingram et al., 2018; Ruffino et al., 2021), which is considered the preferred method of assessing the quality of motor execution (Shmuelof et al., 2012). We propose that at least part of imagery's apparent reliance on perceptual and cognitive functioning is due to the use of experimental tasks that challenge those functions and do not adequately challenge movement execution.

We recently demonstrated that motor imagery is indeed effective for learning to execute a novel motor skill (Ingram et al., 2018). This was achieved using an experimental touchscreen task that involved complex, multi-articular movements that were either randomly generated or repeated, measuring performance via changes in the speed-accuracy function. Importantly, the results could not be explained by perceptual learning alone. Given that motor imagery lacks sensory feedback, the existence of motor learning via imagery appears paradoxical. Sensory feedback is regarded as necessary for motor learning (Wolpert & Flanagan, 2016), as either visual or somatosensory information provides error signals that can be used to make adjustments both during performance and in subsequent attempts (Franklin et al., 2007; Lefumat et al., 2016). However, given that motor imagery may involve a simulation of the executed movement, it is possible that participants have access to the quality of this simulation — consciously or unconsciously — and therefore are able to make refinements to a motor plan based only on a comparison between the intended outcome and the predicted outcome (Dahm & Rieger, 2019).

Indeed, it is well established that sensorimotor control involves forward models that predict the sensory consequences of an action as it unfolds, which allows for corrections earlier than can be explained by sensory feedback alone (Miall & Wolpert, 1996; Wolpert et al., 1995). It has been demonstrated recently that motor imagery also involves the use of forward models to predict the sensory consequences of an imagined movement (Kilteni et al., 2018). Thus, during repeated motor imagery-based practice performance improvements may be driven by comparisons between predicted and intended outcomes of the imagined movement.

Alternatively, the motor-cognitive model of imagery supposes that while overt action is able to rely on unconscious and automatic processes such as forward models, motor imagery is unable to use these processes (Glover & Baran, 2017). Instead, motor imagery uses executive processes to consciously elaborate upon an internal representation of the movement. More complex tasks or those with lower fidelity require greater executive resources to form a representation and therefore give rise to increased movement times compared to overt action.

One can interpret this as implying that rather than imagery involving the processing of predicted error, imagery is instead an exercise in creating an internal representation-of a movement and refining it. That is, as participants are repeatedly exposed to the movement to be imagined, they simply refine their representation-rather than simulate its execution and assess its accuracy. It therefore remains an open question whether imagery-based motor learning is the product of processing simulation error or the product of refining an error-agnostic representation.

To answer this question, we used a previously established experimental task (Ingram et al., 2018) that involves participants replicating a kinematically complex movement pattern at varying speeds on a touchscreen either overtly (overt group) or through motor imagery (imagery group). Varying speeds allowed for the assessment of the speed-accuracy function to investigate the quality of movement execution. The task includes both a repeated pattern assigned to the participant (repeated condition) as the task to be practiced, as well as randomly generated patterns (random condition) that are novel throughout the experiment. While it can be argued that no movement is completely novel as it may be comprised of familiar movement components (e.g., primitives) (Bruno et al., 2015; Giszter, 2015; Ting et al., 2015), more complex movements can be sufficiently novel combinations of familiar patterns. Movement pattern complexity varied in the random condition as well as across participants with respect to the pattern they were assigned. Importantly, after every trial we asked participants in each group (both overt and imagery) to self-report how accurate they believe their performance was. At the end of each block for the imagery group only, we asked participants to rate how vivid their imagery had been in the preceding block of trials. Given that the overt group will have overtly performed the movement and are therefore afforded sensory feedback, their self-reported accuracy should have a strong relationship with their performance as measured by the speed-accuracy function.

However, if motor imagery does not involve error processing and instead involves only the elaboration of a representation, participants self-reported accuracy during imagery may be a function of the number of trials for which they have formed the image, and may be related to their vividness ratings, but will not have a strong relationship with the error you would expect given the speed and complexity of the task. That is, in the imagery group compared to the overt group, the movement pattern will not be sensitive to known drivers of performance (e.g., speed) and self-reported accuracy will have a weaker relationship with performance as measured by the speed-accuracy function, and variability will instead be best explained by their vividness ratings.

Given previous findings that motor imagery involves the use of forward models (Kilteni et al., 2018) and that imagery participants appear to be able to report their accuracy (Dahm & Rieger, 2019), we hypothesized that imagery participants self-reported accuracy will indeed have a strong relationship with their expected error. We also tested whether self-reported accuracy changes across trials in the repeated condition compared to the random condition to investigate whether error processing during imagery evolves similarly to overt practice — that is, we hypothesized that imagery is indeed capable of forming novel motor representations in the absence of previous overt experience and updating the representation in an experience-dependent fashion similar to the overt group. Finally, we analyzed whether movement complexity had a differential effect on movement time between groups. Importantly, our experimental task involved variation in the kinematic complexity of the movement pattern rather than altering goals or sensory features of the task or adding interference tasks which may affect processes upstream to motor execution. If motor imagery depends on limited cognitive resources to form and maintain a representation during imagery, increased complexity should increase movement time compared to the overt group. However, if imagery involves forming a representation of the movement and then performing it via a simulation of the movement and assessing its error, complexity may not have a different effect on movement time between groups. Again, we hypothesized that imagery involves error-processing and therefore movement time would not differ between groups.

## Methods

### Participants

We recruited 96 participants with normal or corrected-to-normal vision who self-reported having typical upper body sensorimotor function. Nine participants were removed from analysis due to technical issues with the experimental setup, resulting in a final data set of 87 participants (see 'Statistical Analysis' for a discussion on sample size).

Participants were randomized into two groups with constraints to ensure roughly equivalent enrollment in each. The imagery group consisted of 43 participants, with a mean age of 23.2 years (SD = 4.74), 27 identifying as female; 6 were left-handed, and 1 was ambidextrous. The overt group consisted of 44 participants, with a mean age of 23.8 years (SD = 7.67), 32 identifying as female, and 2 were left-handed. Note that handedness was determined using the Edinburgh Handedness Inventory (Oldfield, 1971), and participants performed the experimental task with their dominant hand, with the single ambidextrous person choosing to perform the task with their right hand. The study was approved by the Dalhousie University Health Sciences Research Ethics Board; written, informed consent was obtained prior to the study onset for each participant.

### Material and Procedure

#### *Experimental Task*

Participants performed a motor task designed to challenge execution of a kinematically complex, multi-articular upper extremity movement, the details of which have been described previously (Ingram et al., 2018). Briefly, participants sat at a 24” touchscreen monitor situated within a black box to reduce environmental distraction and ensure adequate contrast of the stimulus on the screen (Figure 1). Each trial consisted of a stimulus followed by a participant response. The study was performed in a single session with 6 blocks of 20 trials for a total of 120 trials. Imagery group participants performed 5 blocks of imagery trials with a final block of overt trials, and the overt group performed 6 blocks of overt trials.

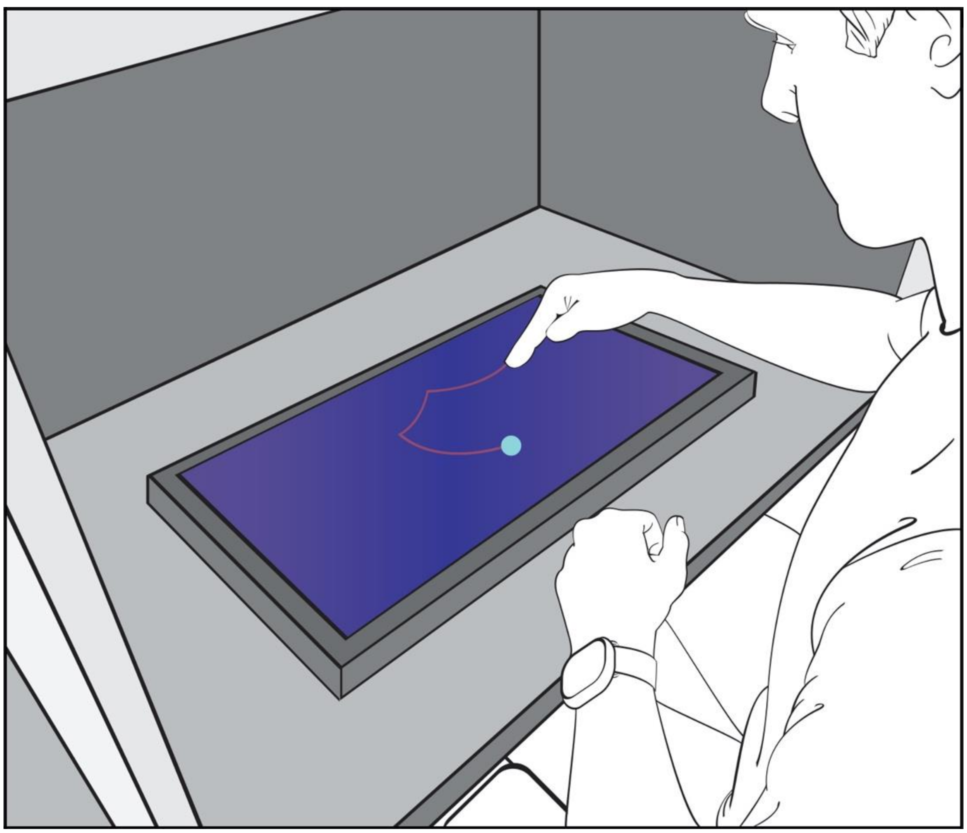

Figure 1. Experimental setup. Note that the tracing on the touchscreen depicted here is for illustrative purposes only and no such feedback was provided to participants. From Ingram et. al. 2019.

Rest between trials was self-paced such that participants began a trial by tapping a button on the screen to begin the stimulus presentation. Stimuli depicted the movement pattern to be replicated by the participant, represented by a white dot that travelled from the starting position to four vertices before returning to the starting position. The starting position was always positioned in the bottom vertical (on the y-axis) half of the screen, with some variation depending on the pattern, and always centered horizontally (on the x-axis). The white dot made curved trajectories between each of the vertices, and always made a clockwise transition from vertex to vertex. Each stimulus pattern therefore consisted of five curved lines. Stimulus patterns could therefore vary by the location of the vertices as well as the curvature of each trajectory between vertices, which gave rise to varying complexity. Complexity for a given trajectory was measured as its sinuosity, defined as the total pathlength of the trajectory, divided by the distance assuming each of the five lines were perfectly straight. Each participant was assigned one of five repeated trajectories (the movement to be practiced) that was presented at an equal ratio with randomly generated trajectories of similar complexity, resulting in 60 “repeated” and 60 “random” trials that were presented randomly but in equal proportions in each block. In either the repeated or random condition, the stimulus was animated in five different movement times (giving rise to varying speeds) in 500ms increments from 500ms (fastest) to 2500ms (slowest). Participants were asked to match both the movement trajectory as well as the speed of the movement on each trial. This allowed for performance to be assessed with a speed-accuracy function.

Immediately upon the completion of the stimulus presentation, participants were cued to respond when the starting position appeared as a red circle. Once the response was initiated by placing a finger on the starting position, the color changed from red to green indicating that the trial was “recording”. Note that as this was not a reaction time task, participants were not asked to respond as quickly as possible — the emphasis was on faithful reproduction of the stimulus pattern and the speed at which it was presented. The movement always began at the starting position and the end of a response was marked by returning to the starting position. Once a trial was complete, participants were not presented with visual feedback other than their own observation of their overt movement — that is, at no time was a tracing of their movement displayed, nor was a tracing of the movement they had to replicate. This was done to reduce the differences between the overt and imagery groups. The imagery group performed the task similarly with the only difference being that once they placed their finger on the starting position, they did not perform the movement. Instead, imagery participants were instructed to engage in imagery of the movement.

At the beginning of the experiment, participants were briefly familiarized with motor imagery, including instructions to perform kinesthetic imagery. The end of the imagery trial was indexed by simply lifting their finger from the starting position as per the overt group. Therefore, movement time was indexed in the same way for each group.

***Self-reported accuracy, actual performance, and expected performance***

For both groups, immediately after each trial participants were asked “How accurate do you think your tracing was?” using a 10-point rating scale where 10 represented perfect accuracy and 1 represented complete inaccuracy. After each block of imagery trials, participants were asked “How vivid was your motor imagery over the last 20 trials?” using another 10-point rating scale where 10 represented perfectly vivid imagery and 1 represented not vivid at all. For each scale, participants responded by tapping the number representing their choice on the touchscreen. During overt trials, error was calculated as the mean of point-by-point Euclidean distance in millimeters (mm) between the stimulus and response trajectories. Both the stimulus trajectory animation and participant response trajectory were sampled at the touchscreen refresh rate of 60Hz, producing a timestamp and x and y coordinate for each sample. However, while the stimulus was animated at a constant speed, natural human movement does not unfold at a constant speed — that is, it is reasonable to expect participants to move faster along straight lines, slower along curves, and slowest around sharp corners. Therefore, dynamic time warping was used to optimally match response trajectories to stimulus trajectories to produce a time-invariant error measure (Giorgino, 2009). To take into account the speed accuracy function (Ruffino et al., 2021), actual performance (that is, measured from physically executed movements during overt trials), was determined by dividing the mean speed by the mean error for each trial, thereby producing an intuitive positive number for "better" performance.

Given overt movement does not occur during imagery it was not possible to calculate actual error for imagery trials. However, for every imagery trial the speed and complexity of the stimulus pattern is known, as well as when it occurred in the experiment (trial number) and what trial type it was (repeated vs. random). Therefore, we used these variables as well as actual performance captured in overt trials to build a model that allowed us to predict expected performance in both overt and imagery trials (see statistical analysis below). Importantly, this model included the final block of the imagery group which involved these participants performing the movement overtly. This allowed for the inclusion of participant level variability in predictions of imagery participants expected performance.

**Statistical analysis**

Bayesian estimation with uncertainty was adopted to perform statistical inference using hierarchical models in all analyses described below. For readers less familiar with Bayesian statistics we highly recommend the recent review by Kruschke and Liddell (Kruschke & Liddell, 2018), and offer a technically imprecise but pragmatic interpretation of the 95% credible interval (from here on referred to as the 95% CI) as being similar to the frequentist 95% confidence interval, where for a given effect an interval that does not include zero can be considered “statistically significant”. Similarly, $R^2$ values with their own 95% CI can also be derived through Bayesian statistics (Gelman et al., 2019). For ease of interpretation, all variables were scaled to the observed data such that their mean value was zero and standard deviation was one. Here our Bayesian models used weakly informed priors equivalent to assuming the mean would fall somewhere within 10 standard deviations of the data observed. Analyses were carried out using the statistical software R.

In employing Bayesian parameter estimation we opted to use an approach to achieve similar ends to guidelines for reporting of Bayesian analysis (Kruschke, 2021). With respect to the topic of power and precision, we sought not to make one-off decisions (i.e., accept or reject the null hypothesis) with attention to the risk of decision errors (i.e., type 1 and 2 error), but instead to convey the relative credibility of the continuum of hypotheses and effect sizes captured by the generative model structure employed, credibility that derives from the application of Bayes rule to use whatever information is present in the data to update beliefs that begin from a weakly-informed and effect-sign ambivalent priors, yielding a multivariate posterior distribution. These posterior distributions were then interpreted by describing effect sizes (i.e., Cohen’s *d* definitions of small (0.2), medium (0.5) and large (0.8)) and their 95% CI, where an effect was interpreted as “significant” if the 95% CI did not include zero. This provides the reader with an intuitive reading of the statistical results, whereby the described effect (e.g., a beta coefficient) indicates the size of the effect and the 95% CI indicates uncertainty and whether the effect is “significant” (not zero; see Supplemental Material 1 for details).

To test our first hypothesis that imagery participants will show a relationship between their self-reported accuracy and expected performance given the stimulus characteristics, we first built a model to predict expected performance. First, a hierarchical regression model was built such that the dependent variable was actual performance (which already took speed into account, as defined above), and independent variables including complexity, trial number, trial type (that is, whether the trial was for a repeated or a random pattern), and with participant included in a hierarchical fashion as a random variable (see Supplemental Material 2 for model details and summary results). As our previous work using this experimental task demonstrated that performance improves on repeated trials relative to random (Ingram et al., 2018), we included an interaction term for trial number and trial type. This model was fit using all overt trials, including all trials from the overt group and the final block of the imagery group. This model was also used as a manipulation check to ensure actual performance improved across trials on the repeated relative to the random pattern.

This model was then used to predict expected performance on all trials including both overt and imagery trials. This allowed for several follow up regression analyses to be conducted on self-reported accuracy: a) self-reported accuracy predicted by actual performance on overt trials, b) self-reported accuracy predicted by expected performance on overt trials, c) self-reported accuracy predicted by expected performance on imagery trials, d) self-reported accuracy predicted by expected performance and self-reported vividness on imagery trials, and e) self-reported accuracy predicted by expected performance on any trial but with condition (overt or imagery) included as independent variable as well as the interaction between expected performance and condition. Results from regressions a) to c) were interpreted by comparing $R^2$, while results from regression e) were interpreted by assessing model estimates of population-level effects, especially the interaction term to determine whether conditions differed in their relationship between self-reported accuracy and expected performance. Regression d) was assessed using both methods. That is, the difference in $R^2$ between c) and d) was interpreted to determine whether vividness explained a significant portion of additional variance in self-reported accuracy when added to expected performance, and the model estimates from d) were interpreted to comment on the size of effects for each variable and whether they interacted.

To test our second hypothesis that imagery can be used to practice a novel movement and update the representation in an experience-dependent fashion, we performed a regression analysis. Self-reported accuracy was the dependent variable and independent variables included condition (imagery or overt), trial type (repeated or random), and trial number. All possible interactions and main effect terms were included, and participant was included as a level in the hierarchy. Of primary interest was whether there existed conditional effects (imagery versus overt) on the interaction between trial number and trial type (that is, the way performance on repeated trials diverges from random trials).

To test our third hypothesis that imagery would not differ from overt movement (the overt condition) with respect to how complexity affects participants ability to match the movement time of the stimulus, we performed a final regression analysis. Here actual movement time (which was measured in both overt and imagery conditions) was included as the dependent variable, and independent variables included the stimulus animation time (which prescribed the target movement time for each trial), complexity, and condition (imagery or overt). Again, all possible interactions and main effect terms were included, and participant was included as a level in the hierarchy. Here our primary interest was again whether a conditional effect (imagery versus overt) existed for the interaction between stimulus animation time and complexity.

For all statistical analyses, variables were scaled to a mean of 0 and standard deviation of 1, which aids in interpretation of statistical results especially when variables are measured on different scales (e.g., comparing performance with self-reported visual analogue scores). This allowed for convenient interpretation of estimated means as reflecting Cohen's *d* effect sizes.

**Transparency and Openness.** Analysis code and those related to the experimental task are openly available online (https://github.com/LBRF/DEMI_Analysis_Pipeline and https://github.com/LBRF/TraceLab). Data is available upon request to the corresponding author. The study was not pre -registered.

# Results

## Self-reported accuracy is correlated with expected performance

Regression analyses demonstrated that actual performance improved across time in repeated relative to random trials (see Figure 2), but this interaction effect was small and credibly included zero (Cohen's *d* = .04, 95% CI -.01 to .09). This finding is in line with our previous work with this experimental paradigm that changes within session are modest but become material across multiple sessions (Ingram et al., 2018). Complexity had a small negative effect on actual performance (Cohen's *d* = -.08, 95% CI -.11 to -.06).

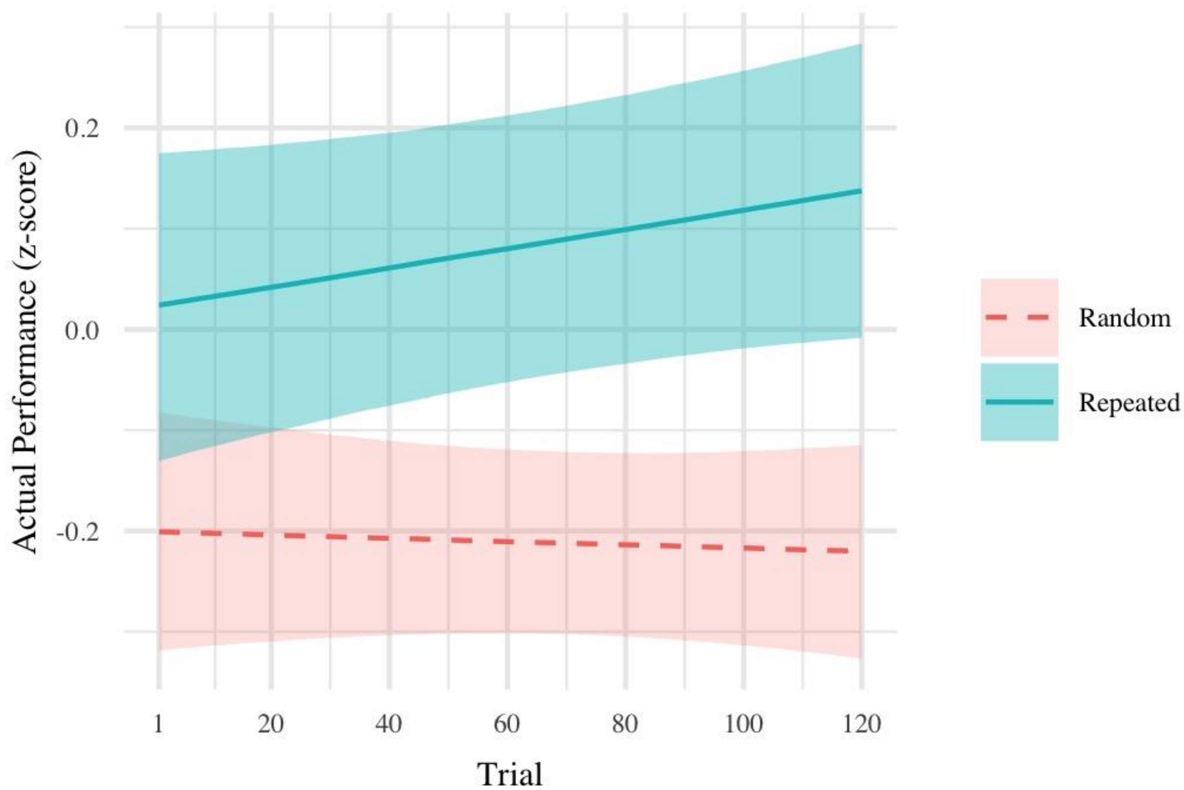


Figure 2. Conditional effects of trial number by trial type (repeated (solid line) versus random (dashed line) on actual performance during overt trials. Lines represent mean and ribbons depict

95% credible interval as estimated by the regression model, not including random effects for clarity. Actual performance z-scored to aid in interpretation.

The first model was used to predict expected performance on all trials (both overt and imagery) to allow for subsequent regression analyses. As a manipulation check, we first investigated whether self-ratings of accuracy correlated with actual performance. Indeed, self-rated accuracy and actual performance positively correlated with an $R^2$ of 0.48 (95% CI: 0.46 to 0.49) which validated that self-reported accuracy was a sensible measure to use for subsequent analyses. Next, we used regression analyses to investigate the correlation between self-reported accuracy and expected performance in each group separately. In the overt group, self-reported accuracy was positively correlated with expected performance ($R^2$ = 0.51; 95% CI: 0.50 to .52). Similarly, in the imagery group, self-reported accuracy was also positively correlated with expected performance but with a slightly weaker relationship ($R^2$ = 0.45; 95% CI: 0.44 to 0.47). A subsequent regression adding self-reported vividness ratings explained an insignificant amount of additional variance ($R^2$ = .47; 95% CI: 0.46 to 0.49) and demonstrated that vividness had only a small effect on self-reported accuracy (Cohen's *d* = .20; 95% CI: .11 to .29) compared to the large effect of expected performance (Cohen's *d* = .97; 95% CI: .64 to 1.31) and the two factors did not interact (Cohen's *d* = .08; 95% CI: -.09 to .26). Importantly, while the $R^2$ values were different between groups, a subsequent regression that included both groups demonstrated that the positive slopes (that is, the beta coefficients for the group by expected performance interaction) were not significantly different between groups (Cohen's *d* = .07, 95% CI = -.13 to .29). However, there was a significant main effect of condition indicating that subjects performing imagery rated their accuracy higher (Cohen's *d* = .51, 95% CI = .36 to .65; Figure 3. These results suggest that participants performing motor imagery are capable of imaging movements with a level of performance aligned with the demands of the task (e.g., the speed and complexity) and their experience with the movement (e.g., trial number and type).

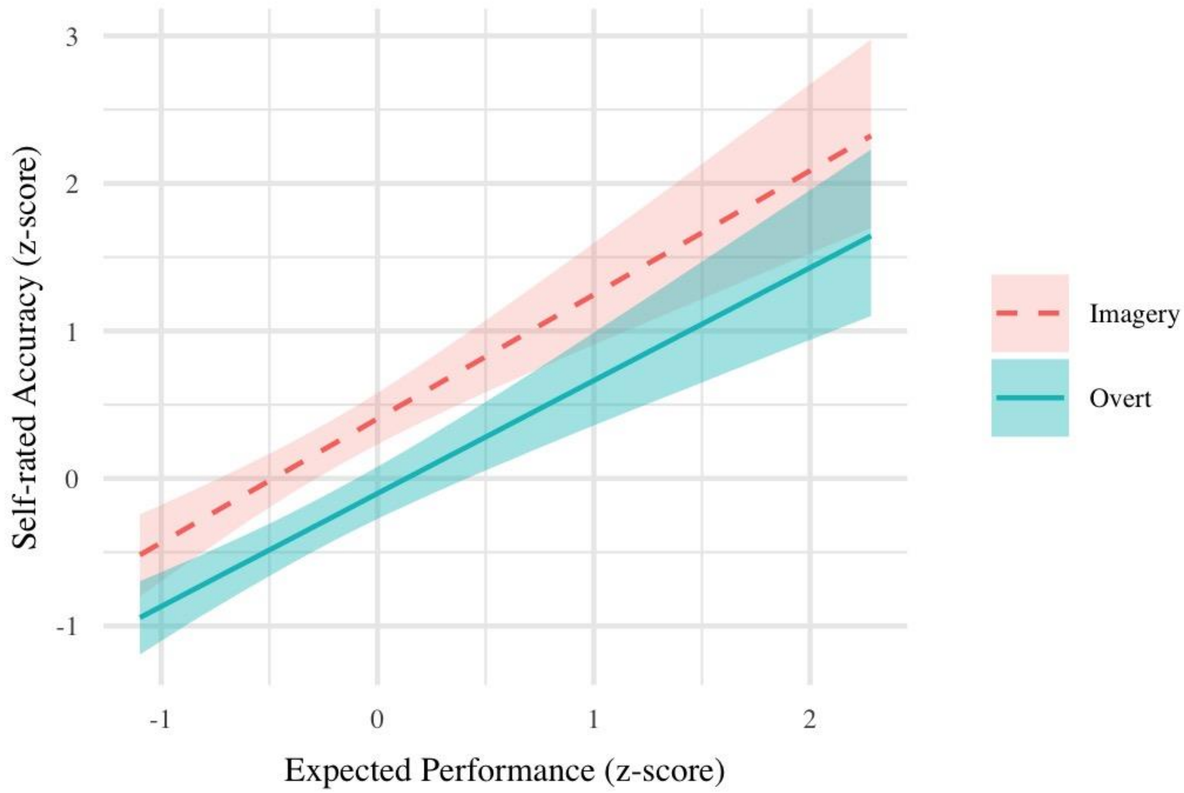


Figure 3. Conditional effect of expected performance on self-reported accuracy for the imagery (dashed line) and overt (solid line) groups. While imagery participants rate their accuracy higher in general, self-reported accuracy is correlated with performance expected given the characteristics of the trial, including the movements complexity, speed, and familiarity (whether the trajectory was repeated or not, and when in the experiment the trial occurred). Lines represent mean and ribbons depict 95% credible interval as estimated by the regression model, not including random effects for clarity. Z-scores presented to aid in interpretation.

**Self-reported accuracy improves with experience**

Next, we investigated whether self-reported accuracy changed across time and whether this was different between the overt and imagery groups (Figure 4). Regression analyses demonstrated a significant interaction between trial number and trial type, where repeated trials improved (i.e., self-reported accuracy increased) while random trials did not (Cohen's *d* = .10, 95% CI = .05 to .14). There was a main effect of condition, where participants reported greater accuracy during imagery compared to overt trials (Cohen's *d* = .58, 95% CI = .45 to .71). Importantly, there were no significant interactions between condition and any other factor — including a lack of a three-way interaction between condition, trial number and trial type (Cohen's *d* = -.04, 95% CI = -.12 to .04). These results suggest that imagery is capable of creating a never before experienced movement representation and updating it with repeated practice, improving accuracy as one would expect during training that occurs through overt practice.

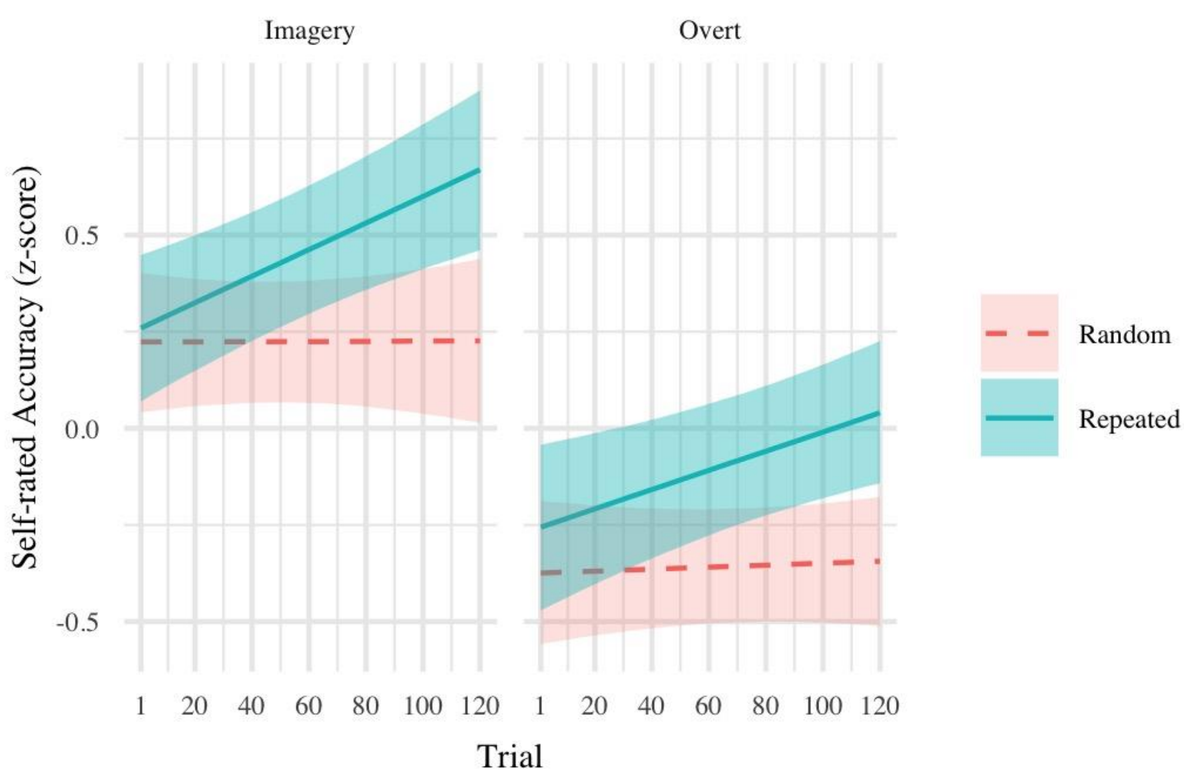


Figure 4. Conditional effects of trial number by trial type (repeated (solid line) versus random (dashed line) on self-reported accuracy for the imagery and overt groups. The imagery group

consistently rated their accuracy higher but demonstrated the same relationship with explanatory variables as the overt group, demonstrating that repeated movement patterns improved across trials compared to novel (random) movement patterns. Lines represent mean and ribbons depict 95% credible interval as estimated by the regression model, not including random effects for clarity. Self-reported accuracy presented as z-score to aid in interpretation.

**Kinematic complexity did not influence imagery movement time**

Next, we investigated whether kinematic complexity had a different effect on each group with respect to their ability to match their movement time to the animation time of the stimulus. Regression analysis demonstrated that generally participants matched their movement time to the stimulus movement time well ($R^2$ of whole model: 0.76; 95% CI: 0.76 to 0.77) and the main effect of stimulus movement time on response movement time was large and significant (Cohen’s *d* = .72, 95% CI = .68 to .76). However, this was the only significant effect in the model (Figure 5). Importantly, the interaction between complexity and stimulus movement time was not significantly different between imagery and overt conditions (Cohen’s *d* = .02, 95% CI = -.01 to .04). That is, complexity did not have an effect on participants ability to match their movement speed to the task requirements during imagery or overt trials. Furthermore, there was no main effect of condition (Cohen’s *d* = -.05, 95% CI = -.19 to .09), suggesting that imagery trials did not take longer than overt trials. Finally, there was no main effect of complexity (Cohen’s *d* = .01, 95% CI = -.01 to .03), suggesting that increasing complexity did not lead to longer movement times. Therefore, movement time was strictly a function of the stimulus animation time in during both overt and imagery trials.

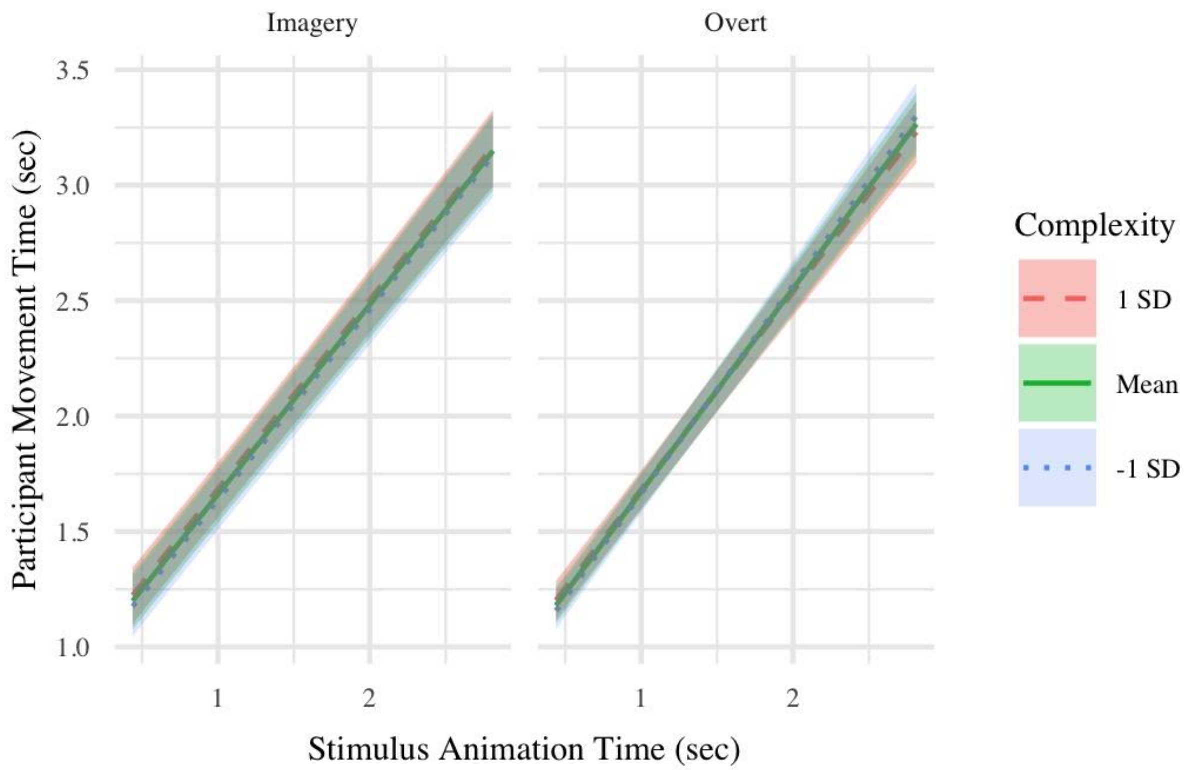


Figure 5. Conditional effects of stimulus animation time on participant movement time for varying levels of complexity (mean complexity observed, mean + 1 SD, and mean - 1 SD) for each group. For both groups, movement time was a function of stimulus animation time only, and not affected by complexity. Lines represent mean and ribbons depict 95% credible interval as estimated by the regression model, not including random effects for clarity.

## Discussion

Here we demonstrate that participants self-reported accuracy during motor imagery of a novel movement task is modulated by known drivers of performance error, including movement speed, kinematic complexity, and experience with the movement. Importantly, vividness of imagery had only a small effect on self-reported accuracy and explained negligible additional variance compared to these drivers of performance error. Further, we demonstrate that this self-reported accuracy is updated with experience, similar to what is observed during error-based motor learning. Finally, we demonstrate that kinematic complexity does not modulate movement time during imagery compared to overt practice, suggesting that participants appear to perform a reasonably faithful replication of the movement during imagined movement execution rather than form and elaborate on an internal representation of the movement during that time. Taken together, these results provide evidence that motor imagery involves the covert performance, or a simulation, of a movement that is not simply an idealized representation of the intended movement. Participants in this experiment were able to recognize and report when their imagined movement was suboptimal, and this report was modulated by known drivers of error: namely the requirement to move faster, or a novel movement that was more complex.

This experiment adds to the growing literature that motor imagery makes use of internal models (Dahm & Rieger, 2019), namely a forward model to predict the sensory consequences of the imagined movement (Kilteni et al., 2018), despite never experiencing the actual sensory consequences. This may explain why motor imagery is capable of driving motor learning of novel motor skills in the absence of sensory feedback (Ingram et al., 2018; Kraeutner, MacKenzie, et al., 2016). While motor imagery lacks sensory feedback necessary to derive an error signal between the observed effects and the intended or predicted effects, imagery may involve the creation of forward models that allow for a comparison between the intended and predicted effects of the imagined movement (Dahm & Rieger, 2019; Kilteni et al., 2018). Repeated imagery may therefore allow for refinement of the forward model or movement representations that depend on it to reduce the difference between the intended and predicted effects. It is likely that actual sensory effects provide more detailed error information, which explains why imagery participants rated their accuracy higher in general throughout the experiment. The lack of additional error information also explains why motor imagery is typically less effective than overt practice for driving performance improvements (Gentili et al., 2010; Ingram et al., 2016; Ingram et al., 2018; Kraeutner et al., 2017; Kraeutner, MacKenzie, et al., 2016; Kraeutner, McArthur, et al., 2020; Kraeutner, Stratas, et al., 2020; Ruffino et al., 2021).

Our results differ from those predicted by theories of motor imagery that posit a lack of involvement by the motor system. Our finding that task complexity did not influence imagery movement times is in opposition to the motor-cognitive model (Glover & Baran, 2017). We suggest that our results are less surprising when considering the nature of the experimental task used in the present study. Here we used a task that emphasizes motor execution (whether performed overtly or via imagery) and de-emphasizes upstream processes such as perceptual processing, goal selection, and motor planning (Wong et al., 2015). While it is likely impossible to completely isolate any one of these processes — they all operate to some degree in parallel — we contend that many experimental manipulations in the motor imagery literature are biased to have their effects on processes other than motor execution. For example, tasks that measure performance using reaction time are likely explained by improvements in perceptual processing of stimuli, goal selection and motor planning, but not improvements in the quality of the movement itself. Similarly, many motor tasks involve experimental manipulations that require online goal selection and motor planning during the movement — for instance, a change to the task requirements during execution (e.g., changing a cursor position to require a correction mid-movement), or the movement requirements are not completely specified until the movement is in progress (common in forcefield paradigms), or an interference task is introduced during the movement. In each case, parallel perceptual processing, goal-switching, and motor plan updates can disrupt the ongoing or subsequent movement.

In the present paper complexity was operationalized as a feature of the movement itself and was not altered once the participant began imagining the movement. Our results imply that once a motor command is ready to be performed, the amount of time needed to imagine it is not affected as long as the participant is allowed to bring the movement to completion without making any additional decisions. However, while our results do not support the motor-cognitive model, they also do not fully support the alternative motor simulation theory. Participants rated their accuracy as significantly higher during imagery compared to overt trials, and our previous work with this experimental task demonstrated that overt training is superior to imagery for driving motor learning (Ingram et al., 2018). What's more, despite our results with respect to complexity, we agree that the literature supports the suggestion by the motor-cognitive model that motor imagery requires greater executive resources (Glover & Baran, 2017), and point to additional literature demonstrating that imagery has a greater reliance on perceptual processing in SRT tasks (Ingram et al., 2016), imagery more readily encodes effector independent information and may not encode effector dependent information at all (Kraeutner, McArthur, et al., 2020), and imagery appears to drive skill learning through different acquisition and consolidation processes compared to overt practice (Ruffino et al., 2021).

It is possible the greater demand imagery imposes on cognitive resources is multi-factorial, and particularly due to the challenge of performing a simulation along with the need to inhibit overt movement. Overt movement involves online feedback control whereby the unfolding movement considers both an evolving forward model and sensory information in real time (Scott, 2016; Todorov & Jordan, 2002). Movement simulation via imagery may be afforded forward models but there is no sensory information. Online control during movement simulation therefore may rely more on the generation of sensory consequence predictions rather than simply receiving this information from the environment, which may require additional processing. Indeed, neuroimaging studies have demonstrated that imagery more consistently involves activation of parietal structures implicated in sensory integration and spatial processing (Andersen & Buneo, 2003; Husain & Nachev, 2007), patients with parietal lobe damage are impaired in their ability to perform imagery (McInnes et al., 2015; Oostra et al., 2016; Sirigu et al., 1996), and imagery-based motor learning is disrupted by inhibitory brain stimulation to these parietal areas (Kraeutner, Keeler, et al., 2016).

Another challenge in performing motor imagery may involve the inhibition of overt movement while utilizing the motor system to perform the simulation (Guillot et al., 2012). The motor-cognitive model posits that for many tasks motor imagery is more susceptible to disruption (e.g., longer movement times) than overt movement because the motor representation is formed and elaborated upon through executive resources. While it is true that frontal cortical regions such as the dorsolateral prefrontal cortex are more consistently active during imagery than overt movement (Hardwick et al., 2018), and that these areas have been implicated in executive functioning (Rottschy et al., 2012), it is also true that they have been implicated in inhibition (Coxon et al., 2016), and it is possible that increasing working memory demands (as per interference tasks) disrupts inhibitory function (Rogasch et al., 2015).

That motor imagery is capable of using forward models to perform a comparison between predicted and intended movement provides evidence that imagery involves the motor system. However, it raises several additional questions. What is the nature of “error” in a motor simulation? When an amateur artist attempts to paint a landscape, it is unlikely that they consider the deficiencies in their work “errors” — it’s not a slip of their brush, but a lack of ability to reproduce the image they intend to. Our work demonstrates that imagery is afforded a sense of accuracy, but it does not necessarily prove that simulations produce errors that are then detected and processed as per overt movement. We propose that motor imagery engages much of the motor system but with important additions and omissions. Obvious differences include the lack of overt movement, which may be reflected in the lack of consistent primary motor cortex activation across neuroimaging studies (Hardwick et al., 2018), given its critical role in executing skilled movement (Shmuelof et al., 2012). As premotor and parietal motor areas are consistently activated during motor imagery — sometimes more so than during overt movement (Hardwick et al., 2018) — motor imagery may involve much the same perceptual processing and motor planning as during overt movement, but with additional movement inhibitory processes as well as greater demands on sensory feedback predictions. We contend that during imagery sensory predictions are used to inform the evolving forward model in the absence of sensory feedback, resulting in iterative use of prediction which may compound uncertainty as a given trial of imagery unfolds (Adams et al., 2013). While this certainly increases cognitive processing demands of imagery compared to overt practice, the human motor system is nonetheless capable of performing these simulations, as if to test and iterate over a motor plan without ever physically experiencing it. As such, a fertile area of future investigation might be developing more sophisticated behavioural tasks that interrogate the computations underlying successful motor imagery and their neurophysiological correlates — which is indeed an active area of investigation in the study of motor control generally (Palmer et al., 2019; Tan et al., 2014; Tan et al., 2016; van Driel et al., 2012).

Funding: This work was supported by the Natural Sciences and Engineering Research Council (NSERC) [RGPIN 2015-04900].

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Figure 1

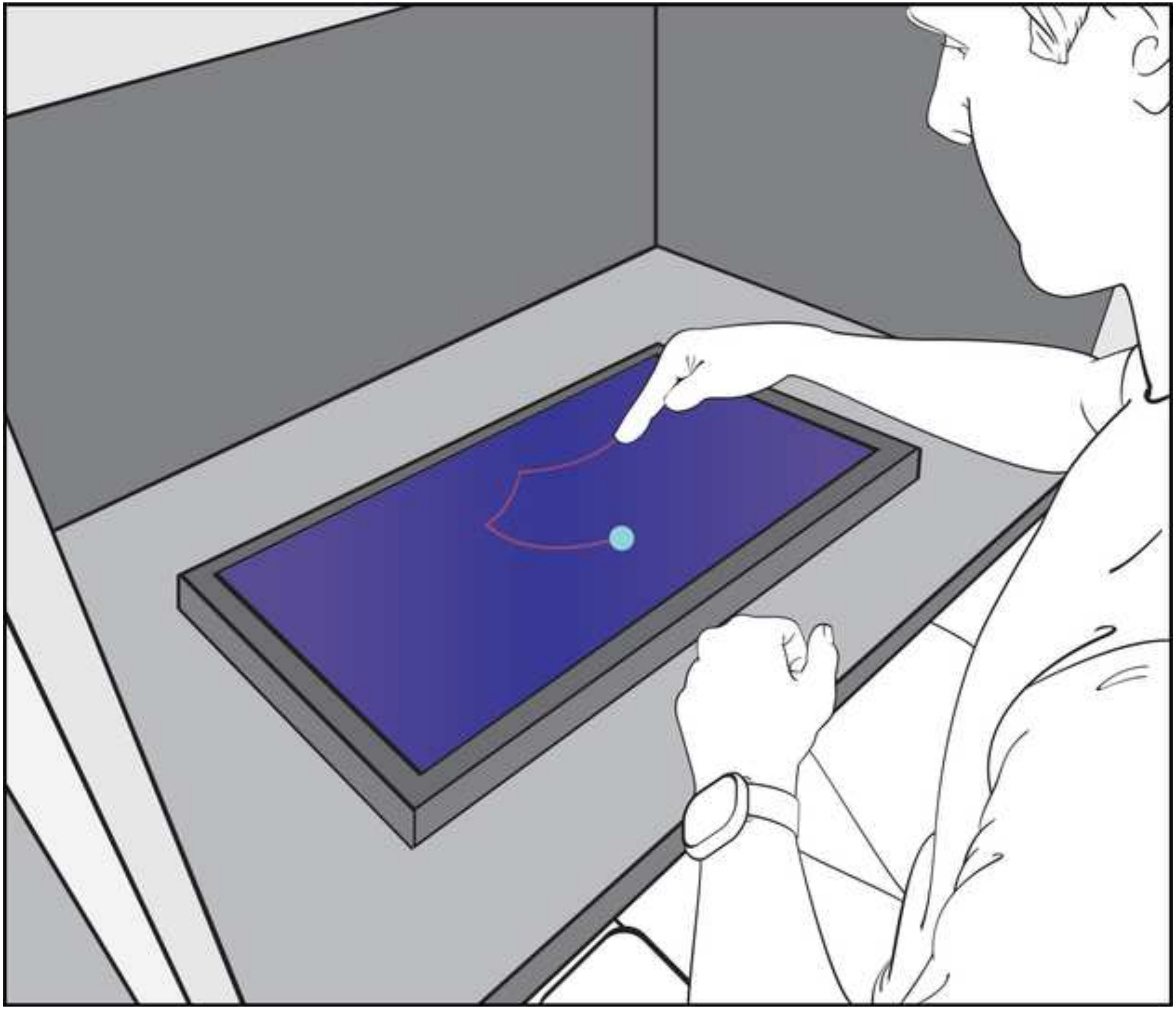


Figure 2

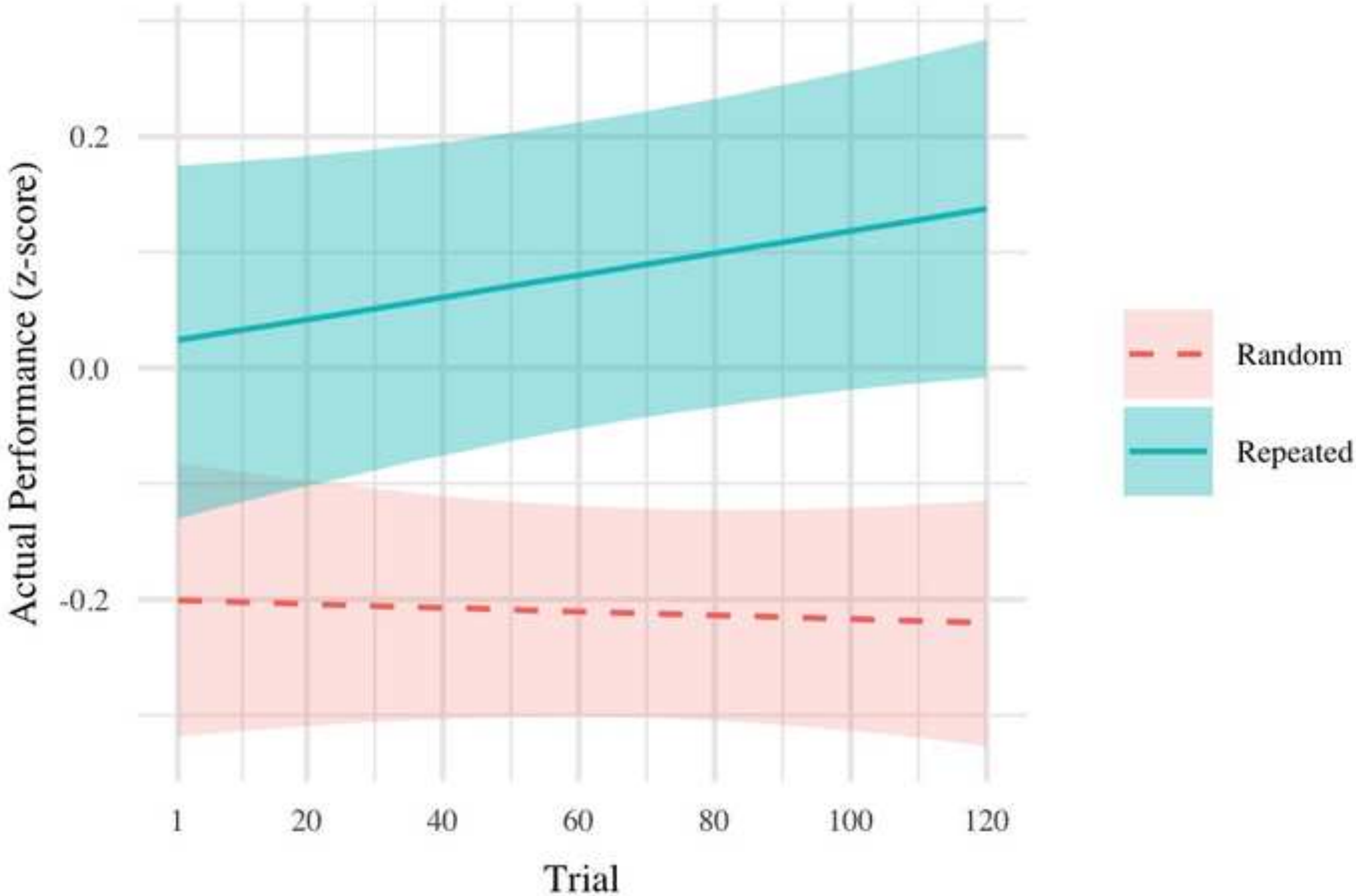
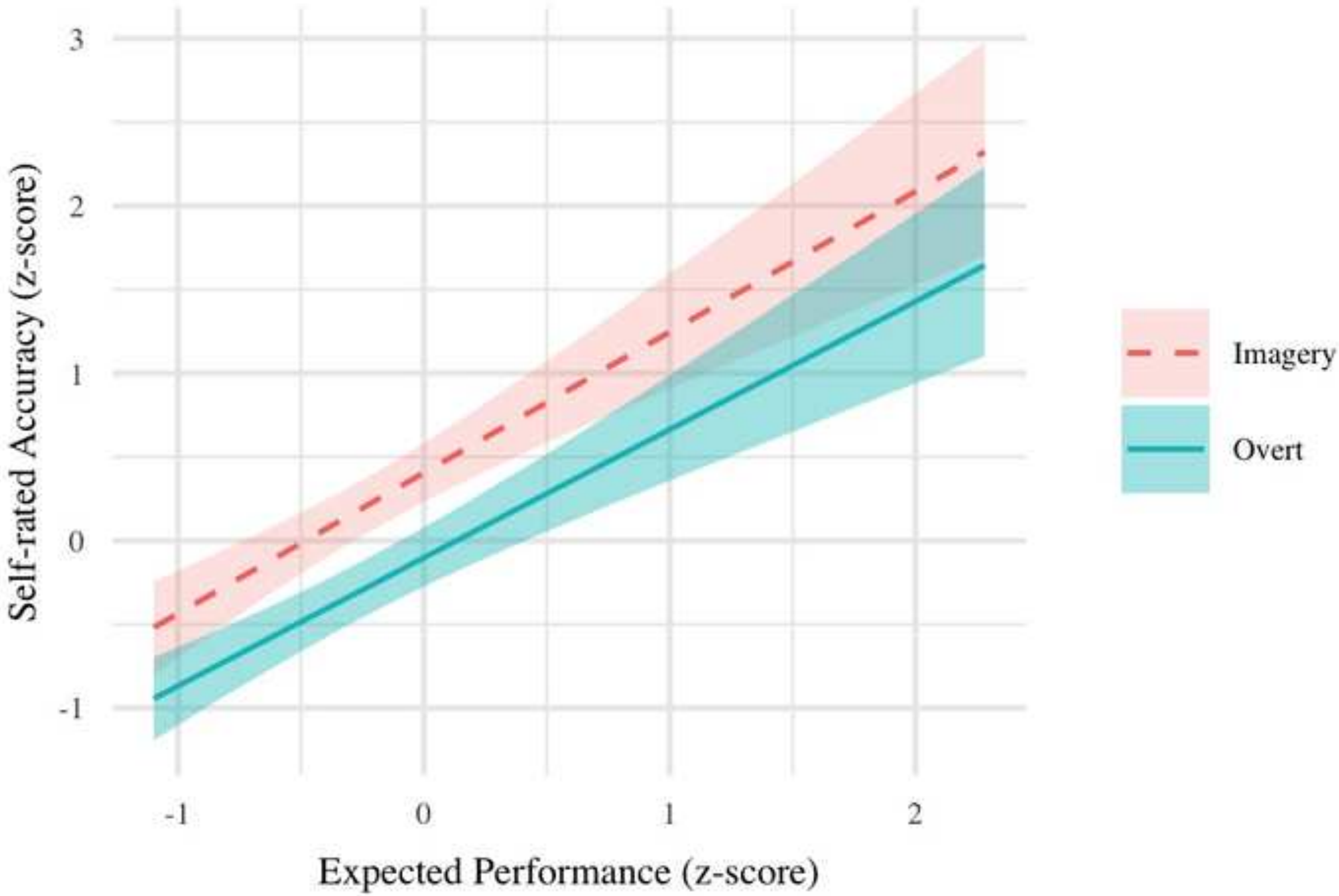

0.2
0.0
-0.2
Actual Performance (z-score)
1
20
40
60
80
100
120
Trial
Random
Repeated

Figure 3



3
2
1
0
-1
Self-rated Accuracy (z-score)
-1
0
1
2
Expected Performance (z-score)
Imagery
Overt

Figure 4

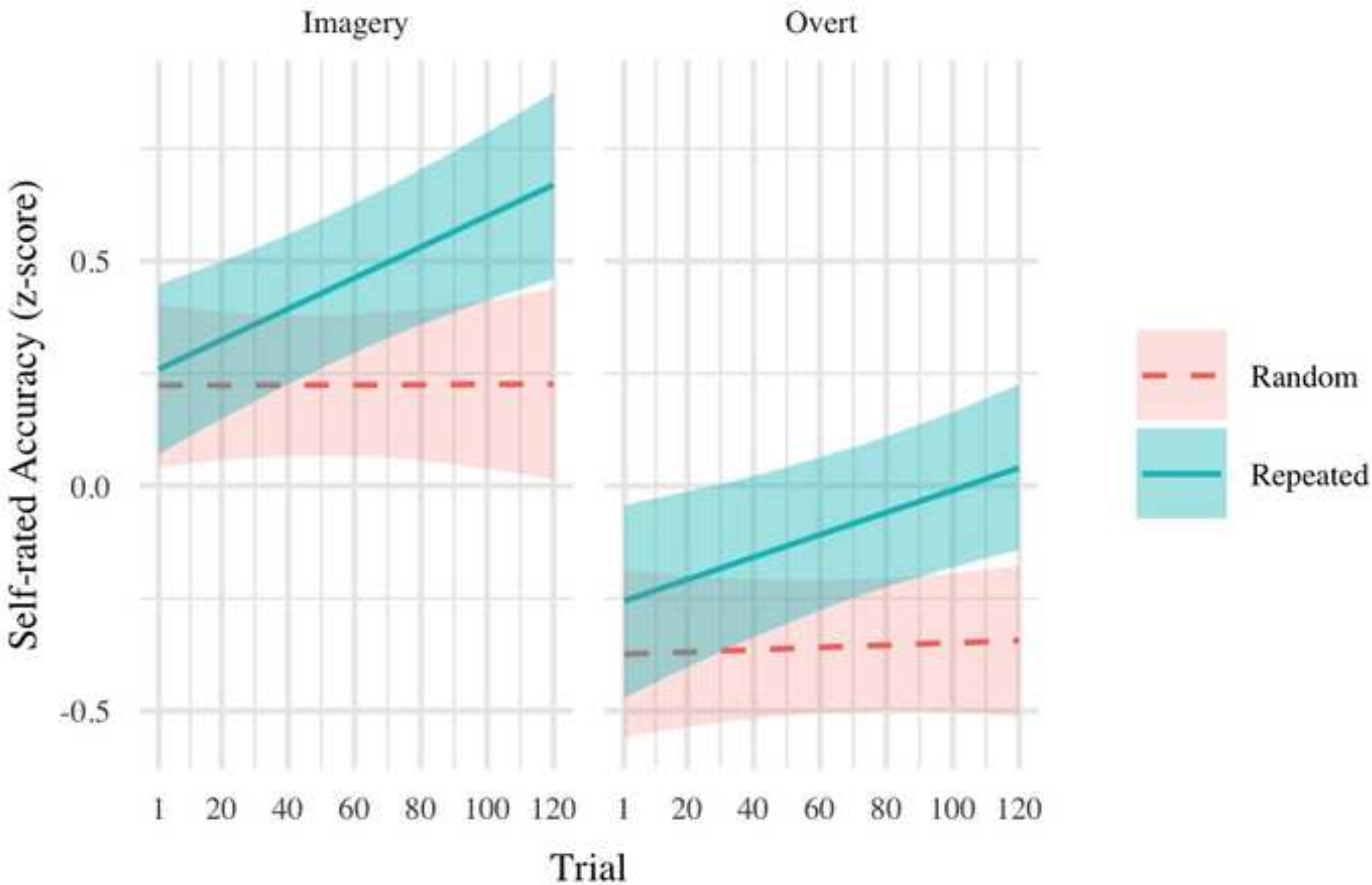

Imagery
Overt
Self-rated Accuracy (z-score)
0.5
0.0
-0.5
1
20
40
60
80
100
120
Trial
Random
Repeated

Figure 5

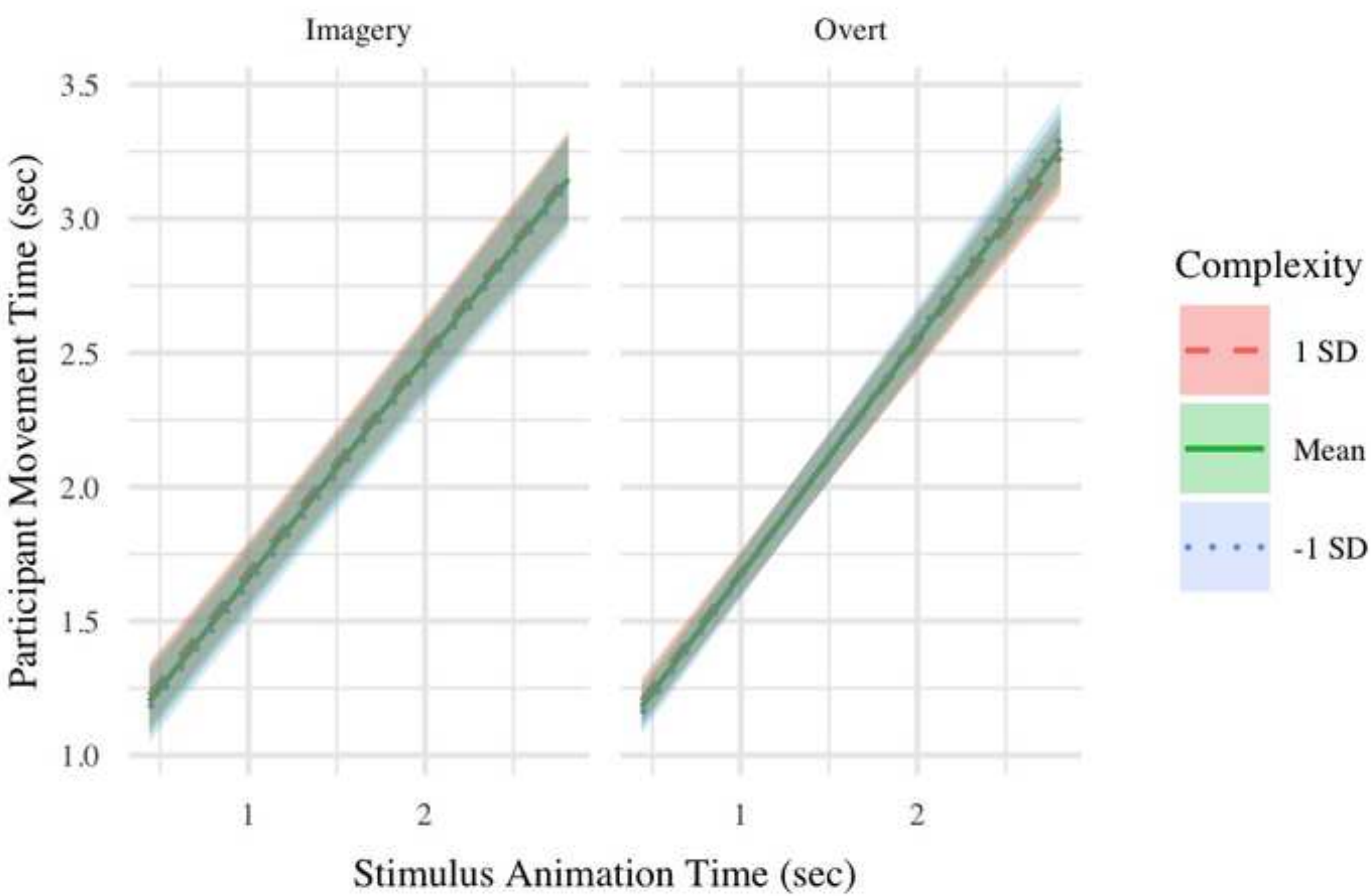

Imagery
Overt
Participant Movement Time (sec)
3.5
3.0
2.5
2.0
1.5
1.0
1
2
1
2
Stimulus Animation Time (sec)
Complexity
1 SD
Mean
-1 SD

FIGURE CAPTIONS

Figure 1. Experimental setup. Note that the tracing on the touchscreen depicted here is for illustrative purposes only and no such feedback was provided to participants. From Ingram et. al. 2019 [19].

Figure 2. Conditional effects of trial number by trial type (repeated (solid line) versus random (dashed line) on actual performance during overt trials. Lines represent mean and ribbons depict 95% credible interval as estimated by the regression model, not including random effects for clarity. Actual performance z-scored to aid in interpretation.

Figure 3. Conditional effect of expected performance on self-reported accuracy for the imagery (dashed line) and overt (solid line) groups. While imagery participants rate their accuracy higher in general, self-reported accuracy is correlated with performance expected given the characteristics of the trial, including the movements complexity, speed, and familiarity (whether the trajectory was repeated or not, and when in the experiment the trial occurred). Lines represent mean and ribbons depict 95% credible interval as estimated by the regression model, not including random effects for clarity. Z-scores presented to aid in interpretation.

Figure 4. Conditional effects of trial number by trial type (repeated (solid line) versus random (dashed line) on self-reported accuracy for the imagery and overt groups. The imagery group consistently rated their accuracy higher but demonstrated the same relationship with explanatory variables as the overt group, demonstrating that repeated movement patterns improved across

trials compared to novel (random) movement patterns. Lines represent mean and ribbons depict 95% credible interval as estimated by the regression model, not including random effects for clarity. Self-reported accuracy presented as z-score to aid in interpretation.

Figure 5. Conditional effects of stimulus animation time on participant movement time for varying levels of complexity (mean complexity observed, mean + 1 SD, and mean - 1 SD) for each group. For both groups, movement time was a function of stimulus animation time only, and not affected by complexity. Lines represent mean and ribbons depict 95% credible interval as estimated by the regression model, not including random effects for clarity.

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