

EXAMINING THE ROLE OF THE INFERIOR PARIETAL LOBE IN MOTOR IMAGERY

by

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DEDICATION PAGE:

Dad, I love and miss you.

Berni, Mom, Mike, Laryssa, Jude, Willow, Kai, Michelle, Beerta, George, Alethia, & Elias,

don't die on me anytime soon.

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## ABSTRACT:

Motor imagery, the mental rehearsal of movement, has been demonstrated to be capable of driving motor skill acquisition. When comparing motor imagery to the more commonly employed motor learning modality, overt execution, the underlying neural activity highlights that motor imagery has markedly more parietal lobe activity, leading to the belief that motor imagery is biased towards the perceptual components of movement. Further, repetitive transcranial magnetic stimulation interventions targeting this area have highlighted the vital importance of the inferior parietal lobes in motor imagery for novel skill acquisition. However, due to the nature of the stimulation, assessing the role of the inferior parietal lobes was not possible. Secondly, the task used in the initial assessments of the inferior parietal lobe were biased towards goal and action selection and the findings could be a result of either the task chosen or an innate property of the modality. This thesis aimed to ascertain the role of the inferior parietal lobe by: 1) stimulating the parietal lobe shortly after the completion of a trial to test if it was involved in the provision of feedback about a trial, and 2) replicating the original findings in the inferior parietal lobe in a complex movement execution task. The inferior parietal lobes did not appear to be involved in the provision of feedback resulting from motor imagery. This finding suggested that either the area is not involved in a role during motor imagery performance or that its importance to learning reflects the task used to originally study the area. However, this second possibility is not supported as a repetitive transcranial magnetic stimulation intervention before training on a kinematically demanding task replicated the original findings related to the importance of the inferior parietal lobe. The combination of findings suggests that the increased parietal lobe activity is necessary for motor imagery rather than being reflective of a task related effect and its role is likely contained to motor imagery performance.

## LIST OF ABBREVIATIONS AND SYMBOLS USED:

**DTW** – dynamic time warping

**HDPI** – highest posterior density intervals

**IPL** – inferior parietal lobe

**KVIQ** – kinesthetic and visual imagery questionnaire

**L\_IPL** – left inferior parietal lobe

**MPE** – maximum probability of effect

**M1** – motor cortex

**RMT** – resting motor threshold

**ROPE** – region of practical equivalence

**RPE** – Reward Prediction Error

**SD** – standard deviation

**SMA** – supplementary motor area

**TMS** – transcranial magnetic stimulation

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## CHAPTER 1: INTRODUCTION

### 1.1 *General introduction:*

Motor behaviours are the fundamental means that are used by any animal to move their body to interact with and affect the environment around them. In order to achieve more effective performance of movement, people adapt to allow them to expend less energy and overcome obstacles or changes in their environment (McNamee & Wolpert, 2019; Todorov & Jordan, 2002). The process of adapting movement to improve its performance is termed motor learning (Krakauer & Mazzoni, 2011; Wolpert & Flanagan, 2016; Wong & Krakauer, 2019). In practice, the study of motor learning encompasses both applied and fundamental research from multiple fields using a variety of methodological approaches (Hardwick et al., 2013; Krakauer, 2006; Maier et al., 2019; Sandbakk & Holmberg, 2017; Scott & Kalaska, 1995). Fundamental research is spread across every permutation of cellular, system and behavioural studies in kinesiology, neuroscience, and psychology to improve our understanding of how the central and peripheral nervous system interface with the muscles of the body to create movement (Cisek & Kalaska, 2005; Dayan & Cohen, 2011; Hatfield et al., 2004; Nakamura et al., 1998; Spampinato et al., 2017; Tanji & Shima, 1994). The applied research captures the widespread uses of motor learning to increase training effectiveness in athletics, music, vocation, and rehabilitation (Goble et al., 2021; Hatfield et al., 2004; MacIntyre et al., 2018; Rohrmeier & Rebuschat, 2012; Sandbakk & Holmberg, 2017).

Learning behaviours is represented at a cellular level by long term potentiation / depression which describes the plastic ability of neurons to alter their physiology based on precise timing and frequency of action potentials (Hebb, 1949; Kampa et al., 2006). Learning on

a global context across the brain is directed by reward prediction errors which are encoded by the dopaminergic neurotransmitter system to represent the level of punishment or reward associated with behaviour (Niv & Schoenbaum, 2008; Roelfsema & Holtmaat, 2018; Schultz, 2002). The provision of rewards is then mediated by attentional resources to identify what cells were used in contribution to the behaviour such that the induced changes only affect the relevant cells (Vartak et al., 2017). The difficulty how learning behaviourally maps to these mechanistic changes is a result of the billions of neurons in the brain, which reduces the practicality of expanding on our mechanistic understanding of learning beyond simple restricted behaviours (J. S. Kim et al., 2014). Advancements in computational neuroscience have begun to address this scope issue by using artificial neural networks to simulate the brain that rely on units which mimic the function of neurons (McClelland & Rumelhart, 1988; Richards et al., 2019). These methodologies are, however, plagued by the credit assignment issue whereby it is near impossible to determine which connections in the network are important for the learned behaviour in a biologically plausible manner (LeCun et al., 2015; Littman, 2015). Therefore, in order understand how motor learning is represented in the brain it is vital to understand these mechanisms in context of the governing behaviour (Krakauer et al., 2017; Lillicrap et al., 2020).

Control of movement can be loosely classified by a serial process with 3 steps: goal selection, action selection and action execution (Krakauer et al., 2019). Goal selection refers to the identification of a location in space that needs to be reached, a desired trajectory to be performed or component of the environment that needs to be manipulated by an effector, the part of the body performing movement (Deubel et al., 1998). Once the goal is selected, a movement needs to be specified such that the effector can be used to achieve its goal with the

least effort (Todorov & Jordan, 2002; Wolpert et al., 1995; Wolpert & Ghahramani, 2000; Wong et al., 2016). Lastly the brain sends out a command to the body to displace the effector from its starting position to the goal of the intended movement (Li et al., 2015). The ability to learn motor skills is derived from these building blocks which can be adapted as a function of practice. Learning is classically thought to be a function of better action selection and improved action execution (Lackner & Dizio, 1994; Shadmehr & Mussa-Ivaldi, 1994; Smith et al., 2006). Improved action selection arises from our experiences whereby the outcome of previous attempts guides our subsequent decisions about which movements are more accurate or efficient at completing its goal (Dolan & Dayan, 2013). Improving action execution relies on continuous monitoring of the effector(s) using a variety of senses, including vision, hearing, and proprioception/touch, to provide feedback about how well the movement is performed (Siegel et al., 2015). This available information can then be used as the tuning signal to correct ongoing movement or to adapt how the movement is performed for a changing environment or the presence of an obstacle (Shadmehr & Krakauer, 2008; Wolpert, 2014). However, movement is not necessary for motor learning.

Motor imagery, the mental rehearsal of movement without overt execution, has the capability of improving performance despite the lack of feedback provided from movement execution (T. G. J. Ingram et al., 2019; S. N. Kraeutner, MacKenzie, et al., 2016). Motor imagery-based motor learning could be likened to a famous scene from the matrix movie where Neo (Keanu Reeves) interfaces with a computer that teaches him all the movements needed to master Kung Fu. In this scene, Neo is unconscious in a chair and his brain simulates a lexicon of “movement programs” that are uploaded into his brain from an external drive. When he awakes



from the simulation, he has instantaneously learned how to move his body in space to perform the entire repertoire of movements taught in the martial arts discipline, and matter-of-factly states “I know Kung Fu”. While the rate of learning is completely unrealistic, in motor imagery the process of learning movement is thought to loosely parallel this fictional program: 1) select a goal for movement (i.e., hit the target), 2) select a movement (identify a punching movement from the program’s lexicon) and 3) “simulate” movement. This cycle would then be repeated iteratively to drive learning. The question is, how?

Historically, motor imagery was thought to be a parallel of physical movement up until the point of movement execution (Jeannerod, 2001). This belief, based on motor simulation theory, has been greatly contested resulting in the creation of several new possibilities that could explain how motor imagery can be used to drive learning, including motor emulation theory, the motor cognitive model and the perceptual cognitive model (Frank & Schack, 2017; Glover & Baran, 2017; Grush, 2004). These theories cite a growing body of neuroimaging and behavioural evidence which has suggested that motor learning via motor imagery relies on improvements to goal/action selection and is biased towards recruiting cortical regions associated with sensory integration for movement (Frank et al., 2014; Hardwick et al., 2018; S. N. Krautner, Keeler, et al., 2016). Specifically, the left inferior parietal lobe (L\_IPL) has been identified as vital to the performance of motor imagery and its function is vital to the acquisition of novel skills via imagery (S. N. Krautner, Keeler, et al., 2016; Lebon et al., 2018; McInnes et al., 2016). Tying the importance of this brain region to a specific role in motor imagery-based movement has been difficult given the methodologies used in the initial investigations and the lack of a clear mechanism for motor imagery-based learning. Additionally,

much of the neuroimaging evidence highlighting the neural networks that underlie motor imagery performance has been generated by studies of movement that are amenable to performance in neuroimaging devices where movement of the head can cause large artifacts in data collection (Hardwick et al., 2018; Puce & Hämäläinen, 2017). A consequence of this decision is that the tasks used in the study of imagery could have conceivably created a bias in the published neuroimaging literature towards patterns of activity that reflect neural resources for control of kinematically simple tasks. Conclusions generalized to motor imagery as a modality could thusly reflect either a bias created by the paradigms used in investigation or a fundamental property of the modality. This ambiguity serves as the motivation for my thesis which aimed to elucidate the role of the parietal lobe in motor imagery and determine if its importance to the network reflects a property of the tasks used to investigate motor imagery or a fundamental property of motor imagery as a modality for simulating movement.

This thesis comprises three studies to address its two purposes. It has been demonstrated that imagery performance can result in self-reported endpoint error, which theoretically could be used as a tuning signal to adapt upcoming attempts at movement, despite the lack of feedback (Dahm & Rieger, 2019a, 2019b; T. G. J. Ingram et al., 2022). It was posited that this error signal could be provided by the L\_IPL in imagery given its role in state estimation (Medendorp & Heed, 2019). Therefore, the first chapter aimed to identify a role for the L\_IPL in the provision of this feedback by using transcranial magnetic stimulation (TMS) to non-invasively affect function of the L\_IPL for a short duration of time after the completion of imagery performance. In the second chapter a novel approach to looking at the outcome measures used to quantify learning in a complex movement execution task was developed.

Typically, the outcome measure used to quantify the success of a motor behaviour is a derivative of error which can differ depending on the behavioural paradigm, including: the distance between a stimulus and the corresponding participant response, errors in applied forces in differing conditions or deviations from optimal kinematics of a movement (Buckingham et al., 2016; T. G. J. Ingram et al., 2019; Nashed et al., 2012). These measures are able to accurately measure improvements in motor execution, however, since movement is absent in imagery, we sought to validate the use of a correlation-based outcome measure that is reflective of changes to action selection. This measure was then used in a study that applied TMS to numerous brain regions to investigate the potential biases introduced by the use of kinematically simple paradigms to measure motor behaviours. Through these chapters we sought to validate the importance of and elucidate a role for the IPL in motor imagery-based learning and clarify if our interpretation of the area's role has been affected by methodological bias. By extension, this information will further our understanding of the neural underpinnings of how motor imagery drives motor learning, allowing people to better leverage the advantages of imagery in its many applications.

## *1.2 What is Learning:*

Learning is a fundamental ability of most living creatures to adapt their behaviour. This behaviour is reflective of a series of coordinated changes across the varying scales of the brain as it acquires new knowledge and is fundamental to most behavioural fields of psychology and neuroscience (Hawkins et al., 2017; Hebb, 1949; Kampa et al., 2006; Ostry & Gribble, 2016; Payeur et al., 2021; Rizzolatti & Craighero, 2004; Rosenbaum et al., 2005; Sherry & Schacter, 1987). At the cellular level learning is reliant on the brain's plasticity; the ability to cause

physiological changes in response to a cell's activity (Hebb, 1949). In this model of learning two neurons can alter their physiology based on the precise timing and frequency of action potentials measured across the synapse between the pre- and post-synaptic neurons (Kampa et al., 2006). If the post-synaptic neuron elicits a response shortly before an action potential from the pre-synaptic cell, then long term depression is induced, whereas if the opposite firing pattern occurs, that is the post-synaptic cell fires after the pre-synaptic cell, then long term potentiation is induced (Bi & Poo, 1998; Sjöström et al., 2001). These changes can persist for extended periods in *in vivo* models providing a physiological mechanism that can strengthen or weaken communication between neurons, which at a larger multi-cellular level could provide a neural representation of a memory in the human brain (Abraham et al., 2002; Cooke & Bliss, 2006).

However, these bi-directional changes in communication on their own would not easily be able to lead to meaningful change without bias introduced by other overarching factors that “steer” learning such as reward-prediction errors and selective attention (Gerstner et al., 2018; Roelfsema & Holtmaat, 2018). Reward-prediction errors refer to the reward or punishment signals associated with unexpected outcomes whereby a disappointing result is encoded by a low reward-prediction error and a gratifying result would be encoded by a high reward-prediction error (Niv & Schoenbaum, 2008). These reward-prediction errors steer learning towards or away from an outcome using the dopaminergic system to communicate the result, which is conferred globally across the brain (Roelfsema & Holtmaat, 2018; Schultz, 2002). Lastly, selective attention gates learning whereby, somewhat logically, humans learn more efficiently when we pay attention (Jiang & Chun, 2010). This effect can be demonstrated in studies using

redundant-relative cue paradigms which test the formation of stimulus-response learning (Ahissar & Hochstein, 1993). In these paradigms multiple stimuli present redundant information which is associated with the correct outcome meaning that participants only need to attend to one cue to learn the task. This is indeed how the task is solved as one stimulus is learned while the others are ignored, indicating that attention can gate which stimuli are learned (Ahissar & Hochstein, 1993). This gating takes the form of an eligibility trace or synaptic tag which is a biochemical marker expressed at the synapse to indicate whether the pre- and post-synaptic neurons will undergo plasticity (Frémaux et al., 2013; Frey & Morris, 1997; Rombouts et al., 2015). While the exact mechanisms of this tagging process have yet to be determined, it is believed that they rely on activation of adenylyl cyclase and phospholipase C signaling cascades as the biochemical marker that indicated that long term depression / potentiation should be induced (Seol et al., 2007). When these two factors, synaptic tagging via attention and reward-prediction errors, are considered in conjunction they highlight a scenario where the union of a highly rewarding or punishing result and the result being “tagged” via selective attention is vital for the induction of learning and, theoretically, long term depression / potentiation (Vartak et al., 2017).

The summation of this work is an updated rule for reinforcement learning that is extended from the principles of Hebbian plasticity originally described in 1949 (see Equation 1.1; Hebb, 1949). In this non-specific equation for long term depression / potentiation, the change in the connection strength between two neurons ( $\Delta w_{i,j}$ ) is predicted by the learning rate parameter ( $\beta$ ) multiplied by functions describing activity in the pre- ( $f_i(a_i)$ ) and post-synaptic cell ( $f_j(a_j)$ ). The consideration of reward-prediction errors and selective attention then

add two new terms onto the model to control for its direction and gate learning respectively (Equation 1.2; Roelfsema & Holtmaat, 2018). In this updated equation the direction of learning is controlled by the sign of the reward-prediction error term ( $RPE$ ), whereby the long-term potentiation is induced by a positive term and long-term depression is induced by a negative term. In contrast, the synaptic tagging resulting from selective attention as derived by higher order brain structures is enacted on the post-synaptic cell ( $FB_j$ ) and ranges from 0:1 to indicate whether or not learning will occur (Roelfsema & Holtmaat, 2018).

$$\Delta w_{i,j} = \beta * f_i(a_i) * f_j(a_j)$$

Equation 1.1: A description of long-term depression / potentiation as suggested by Hebb, 1949.

$$\Delta w_{i,j} = \beta * f_i(a_i) * f_j(a_j) * RPE * FB_j$$

Equation 1.2: A updated description of long-term depression / potentiation including terms for reward-prediction errors and selective attention developed by Roelfsema and Holtmaat, 2018.

### 1.2.1 *Why we do not have a complete bottom-up understanding of learning:*

Given our understanding of how learning occurs at a cellular level, one might be led to believe that there is a robust mapping of learning at this level to behaviour, however this is far from the case. Some of the most difficult questions to answer pertain to the mapping of cellular level changes to the behaviours they hope to explain. These two approaches, “bottom up” (discovering cellular mechanisms explaining higher order behaviours) and “top down” (using behaviour to infer what is happening at a system or cellular level) are often considered independently without regards for one another leading to interpretations of mechanisms that

contradict observed behaviours and behavioural theories that are improbable given the structure and function of neurons. As such, there is a need to explore the behavioural principles that orchestrate plasticity across the brain given our understanding of its fundamental building blocks, neurons (Lillicrap et al., 2020).

The difficulty of using the classical “bottom up” approach is that there are a gargantuan number of neurons, and the approach becomes impractical given limitations of tools available to study neuronal activity in vivo in human participants. In simpler restricted computations such as pattern generators for rhythmic movement and retinal comprehension of movement, intracellular recordings have been used to define exacting mechanisms (J. S. Kim et al., 2014; Marder & Bucher, 2001). However, as the functions being investigated become more complicated and the number of cells in the network grow it becomes harder to use these methods to define a precise mechanism (Richards et al., 2019). With recent advancements in computational neuroscience the ability to abstractly define a ruleset that defines learning has provided a methodology to simulate what might be happening in the brain when we learn a skill. This process revolves around using an artificial neural network to simulate the brain by using units that try to mimic the function of neurons (McClelland & Rumelhart, 1988). These artificial networks are defined by user set methods and rules (structure, goal, reward, weightings) that delineate how the artificial neural network can learn, including reinforcement learning and deep learning (Richards et al., 2019; Williams, 1992). As such, if a model is trained to accurately represent a complex behaviour such as human movement it could potentially be used to provide insight into how the brain co-ordinates the changes seen in a small number of cells to the millions of neurons needed to control and learn complex skills (Mathis et al., 2018).

This approach however is mired by one critical issue: determining which connections in the network are important for the learned behaviour. This is termed the credit assignment issue (Littman, 2015). There are several methods to account for this in an artificial neural network, however the most successful method of resolving this issue “back-propagation” has been historically believed to be biologically implausible (Crick, 1989; LeCun et al., 2015). It was only recently that this concept was revisited to highlight a potential avenue around the credit assignment issue in a biologically plausible manner by using a novel spike-based learning rule that is defined by known properties of dendrites, activity at the synapse and synaptic plasticity (Payeur et al., 2021).

By grounding this advancement with physiology represented in equation 1.2, Payeur et al., highlights a potential mechanism that can simulate learning in the brain (Payeur et al., 2021; Roelfsema & Holtmaat, 2018). The physiology this advancement aims to represent is presented visually by Roelfsema and Holtmaat (2018) in the context of movement, whereby information about the stimulus is encoded by the sensory cortices and communicated to the motor cortex (M1; Figure 1.1 (left); Lamme & Roelfsema, 2000). In turn the M1 uses feedback connections to highlight information from the sensory cortices that are relevant to the process of action selection (Figure 1.1 (middle); Moore & Armstrong, 2003). This function embodies attentional synaptic tagging describing which synapses will undergo plasticity (Jonikaitis & Deubel, 2010; Moore, 1999; Roelfsema & Holtmaat, 2018). These tags would then persist until the subsequent provision of reward-prediction errors such that the direction of the plasticity, long term depression / potentiation, will occur based on the perceived outcome of the task (Figure 1.1 (right); Roelfsema & Holtmaat, 2018). However, the recently conceived spike-based learning



rule has only be defined and validated in a generalized setting and is untested in the context and neurological structure of motor learning and, as such, is just a promising avenue for future research (Payeur et al., 2021). In order understand how motor learning is represented in the brain it is vital to understand its context (i.e., how the brain controls movement), therefore the “top-down” approach needs to be considered (Krakauer et al., 2019).

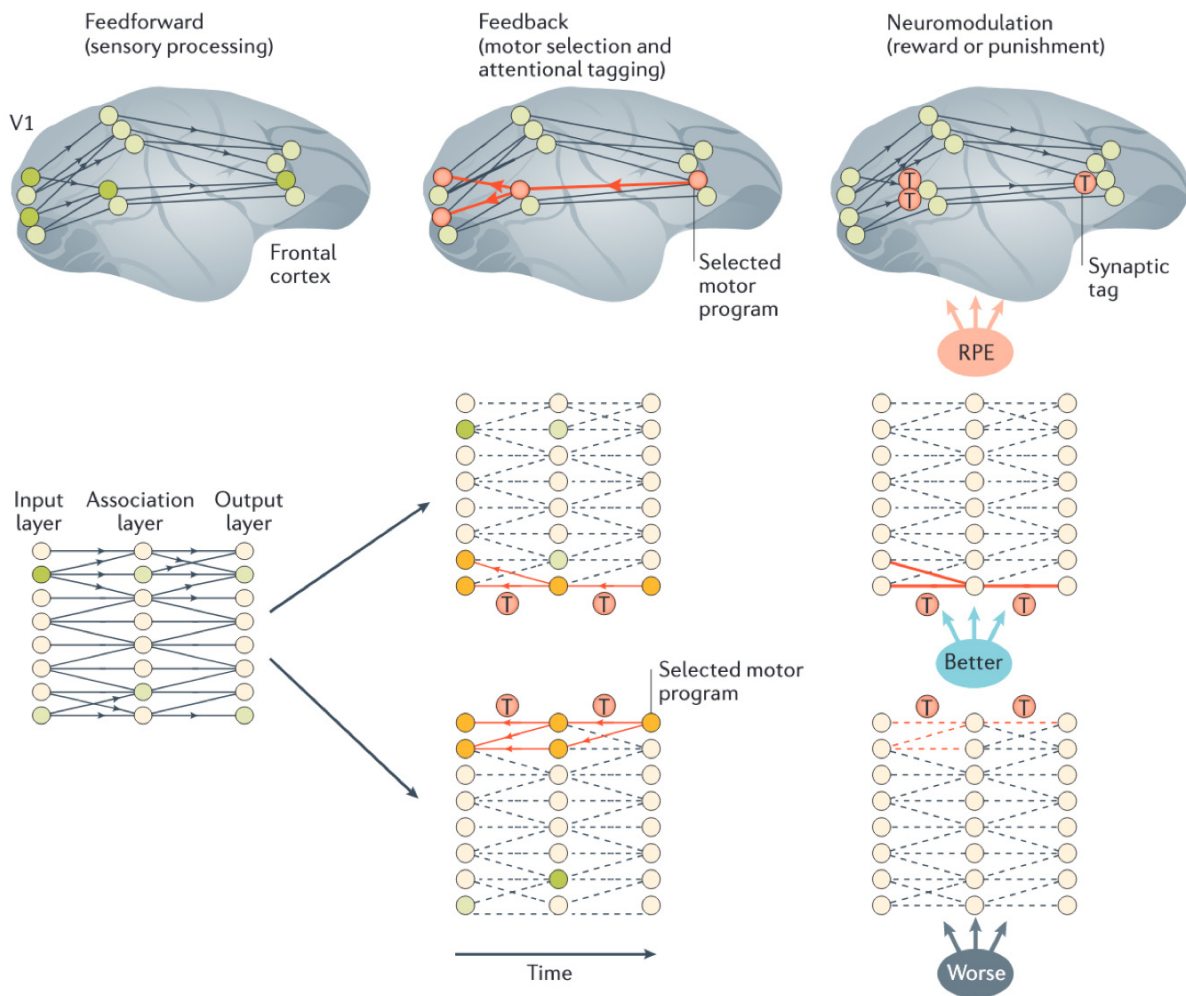


Figure 1.1: A potential mechanism for synaptic plasticity underlying learning in the brain taken from Roelfsema and Holtmaat (2018). The columns from left to right describe the sequential theoretical steps controlling plasticity: feedforward control, feedback control and neuromodulation. The flow diagrams in the bottom row describe a simplified network structure from the sensory inputs (input layer) to the motor cortex (output Layer). In the feedforward column information is passed towards the output layer along the lines with grey arrowheads. Feedback control is then applied from the output layer back towards the input layer, tagging (T) the important signals used to select the movement which will be subject to plastic change (red lines; middle column). In the right column the signal is modulated by outcome of movement (RPE = Reward prediction error, grey = poor outcome, blue

= positive outcome) to determine whether the tagged synapses will be reinforced (red lines) or repressed (red dashed lines; Roelfsema & Holtmaat, 2018).

### 1.3 What is the context for motor learning:

What differentiates motor learning from other forms of learning, cognitive or perceptual, is that the end point is improved movement. While this seems obvious, these different types of learning are likely linked by similar theoretical neural underpinnings governed by the capacity of the brain for plasticity (Cooke & Bliss, 2006; Krakauer et al., 2019). Extending from the model presented in Figure 1.1, there are a variety of contextual factors that are not considered: 1) What is the effect of pre-existing knowledge on this system, 2) How are movements selected and 3) How does this network account for real-time monitoring of movement? These questions add further layers of complexity and obscurity onto the model and in order to garner insight into these questions, the “top-down” approach of mechanistic inference from behaviour needs to be evaluated.

Generally, behavioural investigations of motor learning focus on improvements made to one of three sequential stages that govern the control of movement: 1) goal selection, 2) action selection and 3) action execution which have been informed by a variety of different classes of behavioural tasks (Figure 1.2; Krakauer et al., 2019). The goal selection and action selection stages of this framework are intrinsically linked to define a process of planning a movement that achieves the goal of the task at a minimal cost (Gallivan et al., 2018; Todorov, 2004). In contrast, they are disparate from the action execution stage which pertains to the control of overt movement (Shadmehr & Krakauer, 2008; Todorov & Jordan, 2002). However, the “top down” approach of modelling behaviour has resulted in competing computational theories at each of these stages, goal selection, action selection or action execution, with the goal of accurately

inferring how the brain completes each one (Gallivan et al., 2018; Hadjiosif et al., 2021; McNamee & Wolpert, 2019). A thorough description of the various theories for motor control is important for understanding the framework that produces reinforcement/depression of a behaviour in motor learning, but it is out of the scope of this thesis and not overtly tested in the following chapters. Instead, the most well accepted model will be described to explain which signals the body can use to estimate the accuracy of their movement, which is a vital signal for driving changes in motor behaviour (Krakauer et al., 2019; McNamee & Wolpert, 2019).

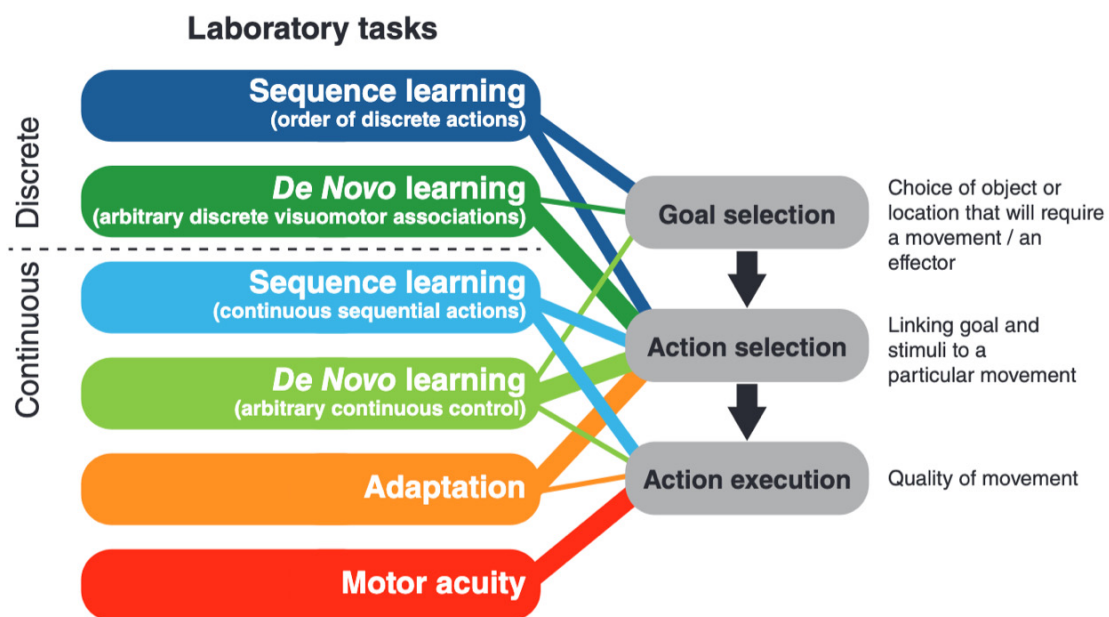


Figure 1.2: A classification for components of movement (right) and the mapping of commonly used classes of behavioural paradigms in psychology and neuroscience (left) taken from Krakauer et al., (2019).

Figure 1.3 outlines the widely accepted model for motor control relating each stage from Figure 1.2 (right) to a concrete example of swinging a tennis racket (Krakauer et al., 2019; McNamee & Wolpert, 2019). The presented model is the culmination of two theories for learning, optimal feedback control and internal models, using a Bayesian framework as a unifying method to communicate the body's understanding of information relating to the

movement (Haith & Krakauer, 2012; McNamee & Wolpert, 2019; Todorov & Jordan, 2002; Wolpert et al., 1995; Wolpert, 2014). The mapping of the stages presented in Figure 1.2 (right) to Figure 1.3 is as follows; the goal selection stage encompasses the Perception and Simulation panels, the action selection stage is akin to motor planning, and action execution is akin to optimal feedback control.

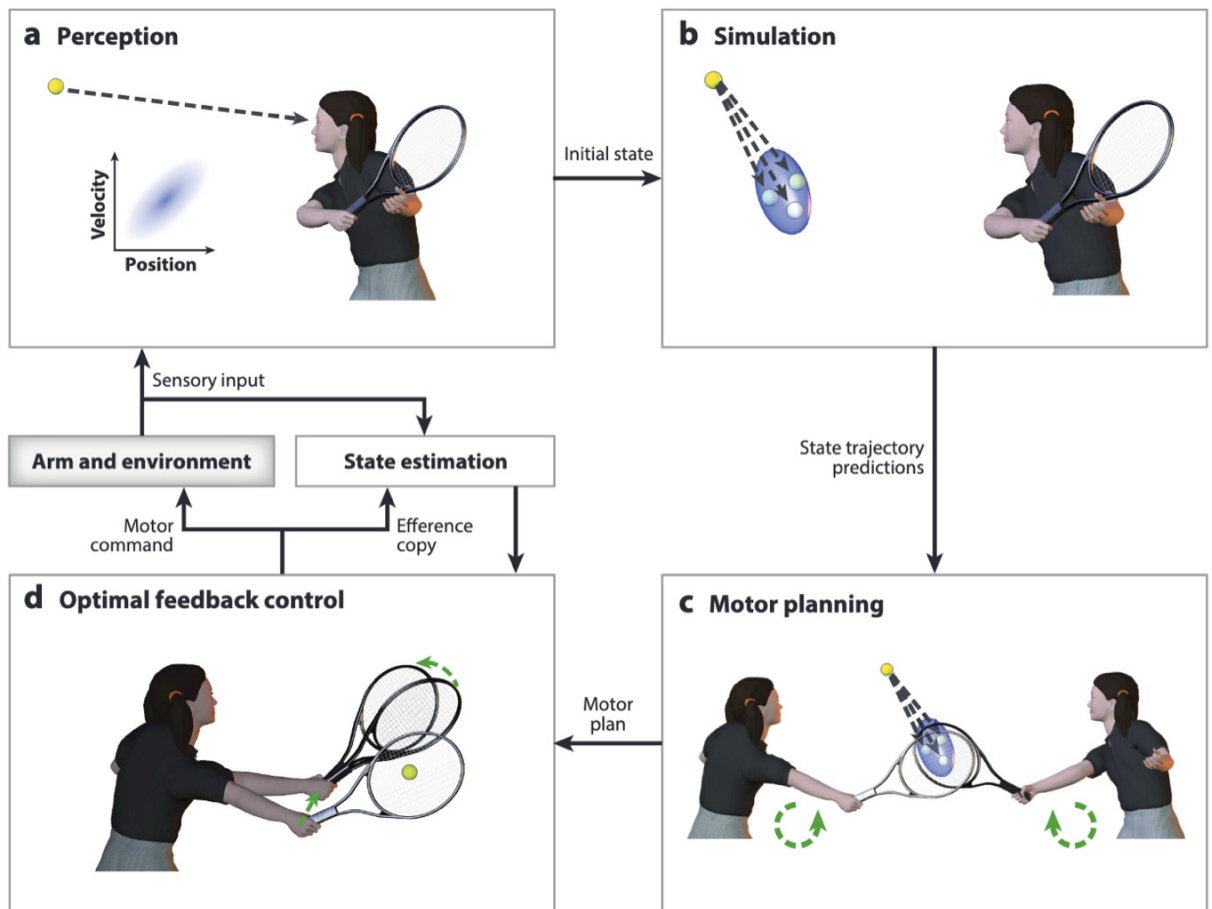


Figure 1.3: A schematic for the stages involved in generating and controlling movement adapted from McNamee and Wolpert (2019). Subplot A demonstrates how sensory inputs to the cortex are used to perceive the endpoint of the movement, the tennis ball, and estimate its position given characteristics such as velocity or rotation that are not directly observable (Subplot A insert). If the object is in motion, then its future state position is to be estimated based on the initial perception of the object such that it can be intercepted by the effector (Subplot B). A motor plan, control policy, is then generated to align the effector with the goal of the movement (Subplot C). Finally, as movement is executed, an efference copy is used to predict where the effector should be and is compared against sensory afference from movement as defined by optimal feedback control to correct movement in real time (Subplot 4 and flow chart).

### 1.3.1 *How do we pick a goal for movement:*

The process of selecting a goal for movement differs considerably based on the context in which the movement is performed, such as the number of potential goals, whether there are competing goals, and identifying if goals need to be sequenced. However, each context arrives at the same outcome, identifying the endpoint for movement (Kaufman et al., 2015; Nashed et al., 2012, 2014; Reichenbach et al., 2014). Regardless of the strategy needed to pick a goal, it first needs to be perceived using sensory information about the state of the environment. This input from sensory receptors contains an amount of biological noise that is overcome by combining sensory information across short time intervals and the union of information from multiple sources, such as vision and audition, to create tight probability distribution of where a point / object of interest is in the surrounding environment (Jazayeri & Shadlen, 2010; Tassinari et al., 2006). Pertinent to the example of hitting a tennis ball, some characteristics of the tennis ball are not going to be observable such as its exact position, velocity, or spin and, as such, these features are estimated using the senses to the highest degree of accuracy possible (see inset of Figure 1.3a visualizing the ball's probable location and speed). If the object of interest is not changing in the environment, then the goal of movement is set, however this is often not the case. If an object is moving then its future position will also need to be estimated using an inferential model whose input is information gathered about the current state of the object (McNamee & Wolpert, 2019). The accuracy of this simulation will depend on the precision of its inputs, that is the sensory information and the duration of time to be predicted to align the effector (or the tool held) with the object of interest, in this case a tennis racket and ball respectively (Figure 1.3). Notably, if an object is stationary then this prediction does not change

the initial state of the object of interest and the simulation of the objects future state is redundant and skipped (McNamee & Wolpert, 2019).

### *1.3.2 How do we select a movement:*

After identifying the movement's goal and endpoint, the prediction of the tennis ball's future position, a motor plan needs to be specified to align the effector or tool, a tennis racket, with it. How the brain chooses what movement to perform defines the degrees-of-freedom problem whereby there are a huge number of effector parameters (such as joint angles, rate of muscle recruitment or effector positions) to optimize in comparison to a much smaller number of parameters needed to explain a task and perform it accurately (Bernstein, 1967). In the example of a tennis swing, this could represent the different variations of a forehand versus backhand shot that could be used to return the ball across the net (Figure 1.3c). Yet despite the near endless possible manners in which to conduct a movement, motor behaviours seem to conform to a similar subset of kinematics/dynamics across individuals, suggesting that the central nervous system is selecting movements on a base set of principles that optimize some component of movement (Domkin et al., 2002; Gallivan et al., 2018; Scholz & Schöner, 1999). The process of making this selection is, as explained by optimal feedback control, done by specifying a control policy and a feedback controller that generates an approximation of the most efficient motor plan to govern how movement will be performed (Todorov & Jordan, 2002). This step is of particular importance to the topic of this thesis, motor imagery-based motor learning, as optimizing the process of action selection is thought to be the primary method used to drive learning via motor imagery given the absence of action execution

(discussed in section How do we learn via motor imagery and all the subsequent chapters). As such, it is worth operationally defining what a control policy is.

### 1.3.3 *What is a control policy:*

It would be natural to think that the motor plan resulting from action selection is a complex spatiotemporal sequence of muscle activations, but completing this task before initiating the movement would be computationally nearly impossible given the degrees-of-freedom problem (Bernstein, 1967; Haith & Krakauer, 2012; McNamee & Wolpert, 2019). As such, control policies are an accepted representation of a motor plan (Todorov & Jordan, 2002). Control policies take the form of a Bellman equation that look to minimize the metabolic costs incurred over the course of the movement while still achieving its goal, which are defined generally to remain applicable to any state of the effector and movement goal (Todorov, 2004). The value of this distinction is well demonstrated by results of a perturbation reaching task where participants were instructed to use a robotic interface to reach out to a target whose width varied (Nashed et al., 2012). In a subset of trials, mechanical perturbations were applied to the robotic arm resulting in a deviation from the relatively straight trajectory seen in the unperturbed trials (Figure 1.4). Notably, efforts were only made to correct the perturbations in the narrow target condition and not in the wide target condition (Figure 1.4). If the entire trajectory had been specified prior to movement than any deviation from it during subsequent execution would be classified as error to be corrected, which was not the case. The extra energy needed to correct errors in movement was only expended if the error(s) impacted the outcome of movement, as dictated by a control policy. Therefore, improving the accuracy of this control policy is the temporally first encountered mechanism that can be used to improve movement

performance (see Improving action selection below).

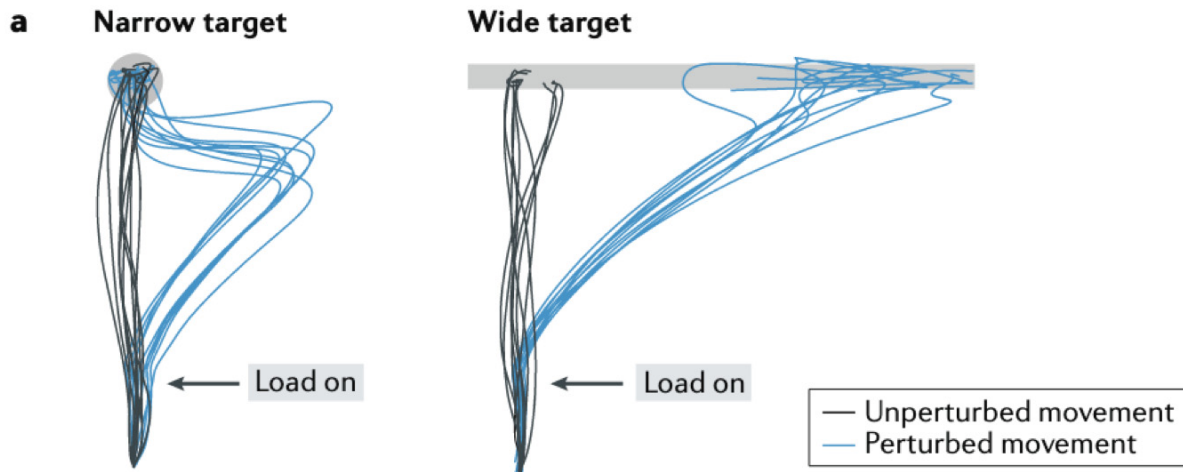


Figure 1.4: Results of a perturbation reaching study by Nashed et al., (2012). Black trajectories are a visualization from unperturbed trials and blue trajectories are from trials where perturbation forces were applied to the robotic arm used to complete the movement. Notably, perturbed movements were only corrected if they affected the likelihood of a positive outcome on the task. This figure was taken from Gallivan et al., (2018), which was adapted from the original study.

#### 1.3.4 How do we execute movement:

Once the control policy for movement is specified, the movement is initiated and monitored for error to ensure it can be performed as accurately as possible and adjusted if needed to try and achieve the movement's goal (Hadjiosif et al., 2021; Shadmehr & Krakauer, 2008; Todorov & Jordan, 2002; Wolpert et al., 2011). With regards to our tennis swing example, once the player begins to move the racket, they monitor their swing to ensure they will still contact the ball (Figure 1.3d). If the movement seems inaccurate, then the angle of the racket can be changed to return the ball over the net (Figure 1.3d green arrow). The most widely accepted theory of how movement is controlled in an online fashion is optimal feedback control which use forward models to generate predictions about movement in absence of sensory afference (Desmurget & Grafton, 2000; Miall, 2003; Miall & Wolpert, 1996; Todorov & Jordan,



2002). The theory of optimal feedback control has only been very recently questioned in favor of motor control theories such as adaptive dynamic programming and direct policy learning which question the use of forward models in motor control (Bian et al., 2020; Hadjiosif et al., 2021). In these newer models perceived errors during movement directly update the control policy (Bian et al., 2020; Hadjiosif et al., 2021). Optimal feedback control dictates that as motor commands are executed, a copy of the motor command, termed the efference copy, is maintained and passed to a forward model which translates the efference copy into a prediction of the effector's future position (Figure 1.3 efference copy line; Desmurget & Grafton, 2000; Miall, 2003; Todorov & Jordan, 2002). The resulting prediction is compared to the sensory afference from movement in a process termed a state estimation (Figure 1.3 state estimation box; Todorov & Jordan, 2002). If there is a mismatch between the signal used in state estimation, a sensory prediction error is recorded and the control policy is re-assessed to send a new, adapted motor command to the effectors (Figure 1.3 downwards arrow extending from state estimation; Todorov & Jordan, 2002). In adaptive dynamic programming and direct policy learning the changes to this model suggest that sensory prediction errors occur by comparing either sensory afference directly to the goal of movement to adjust the following motor command (Bian et al., 2020; Hadjiosif et al., 2021). Only if the sensory afference is absent is the prediction of the effector's future position from a forward model used in its place to create a sensory prediction error (Hadjiosif et al., 2021). With respect to motor learning, two signals are generated during action execution that can be used to drive learning. The first is the sensory prediction error, which can be used to reduce the task relevant variability with repeated practice to improve action execution (see Improving action execution below) and, secondly, feedback

about the final outcome of movement can be used to help improve the accuracy of the control policy (see Improving action selection below).

#### *1.4 How are motor skills learned:*

As previously mentioned, motor learning refers to the process of improving skill execution as a function of rehearsing the movement. Learning can be driven by either physically practicing the movement or by mental rehearsal of movement (see sections 1.5 What is motor imagery & 1.6 How do we learn via motor imagery below; Eaves et al., 2016; T. Kim et al., 2017; Krakauer et al., 2019). Gains in skilled performance are realized through two avenues, explicit improvements made to the processes of goal / action selection and implicit improvements to action execution driven from the signals originating in the framework of motor control (Figures 2 and 3). This includes signals derived from feedback about the final outcome of movement and sensory prediction errors generated during movement (Figure 1.3).

##### *1.4.1 Improving the accuracy of the control policy:*

Improvements made to the accuracy of the control policy are dictated by our past experience and previous attempts at a movement (Dolan & Dayan, 2013). Our past experiences of movement generate feedback and guide our decisions about which movements to perform next. This information takes the form of task error, the difference between our expected and attained outcome of a movement, that provides an estimate of the magnitude and direction of error to be corrected or a more generalized knowledge of success or failure if feedback about movement is unavailable (Taylor & Ivry, 2011). These errors are classified as reward prediction errors (see What is learning above) that can guide our understanding of how to execute a task using processes akin to those applied in reinforcement learning (Sutton & Barto, 1998). This

process of trial-and-error learning dictates one's past experience would suggest repeating or avoiding a specific movement and the brain would then generalize an abstracted rule, a control policy, which can be called upon to guide upcoming attempts at the movement (Körding & Wolpert, 2004; Todorov & Jordan, 2002). These reward errors appear to be encoded by neural activity in the striatum whereby the dorsal striatum encodes information about the reward of a completed action, modifying activity in the ventral striatum to reflect what the expected reward will be on a future iteration of the task (O'Doherty et al., 2004; Schultz et al., 1997). These representations can, in turn, be recalled to predict what the expected reward would be for a novel movement goal, which would be vital for goal selection in movements with a choice between two or more potential goals (Barron et al., 2013; McNamee et al., 2013; Padoa-Schioppa & Assad, 2006).

Once the goal of a movement is specified, the control policy would dictate that the body needs to approximate what is the most energy efficient method to accurately complete the movement (Todorov, 2004). The drawback to this approach is that learning a control policy through trial-and-error learning is prohibitively slow and, as such, the suggestion has been made that movement representations are organized in a hierarchy (d'Avella et al., 2003; Haar & Donchin, 2020; Kanai et al., 2015; McNamee & Wolpert, 2019). This suggestion indicates that movement is represented at potentially multiple levels of abstraction where the top of the hierarchy is the control policy that governs action selection, and the lowest level would be each individual component of spatiotemporal series of muscle activation needed for action execution (McNamee & Wolpert, 2019). These two hierarchal extremes, top and bottom, would then be separated by intermediary levels termed motor chunks (Botvinick et al., 2009; Haar & Donchin,

2020; Rhodes et al., 2004). This organization of behaviour provides a potential solution to reduce the degree-of-freedom problem that plagues motor learning and is grounded in behavioural observation from well-studied serial reaction time paradigms (Bernstein, 1967; Verwey et al., 2015). In these paradigms, repetitive practice of a sequence of button presses has demonstrated that if the sequence is long enough, a motor chunk is created in memory to represent a sequential series of movements (Rhodes et al., 2004). This reduces the number of features needed in memory to represent the entire sequence of movements (Verwey et al., 2015). In turn, these chunks could be used to help create the control policy for movements that are novel or not well understood. This mechanism is evidenced by hand path priming effects, where participants complete a reaching movement where obstacles occasionally obstruct straight line movement (Jax & Rosenbaum, 2007). Initial angular offset, the curvature at the beginning of the trajectory, on unobstructed trials increased as a function of likelihood and recency of an obstructed trial (Figure 1.5). This finding demonstrates that our past experiences can cause deviation to the optimal strategy for movement under the circumstances where the sub-optimal strategy for movement appears to be more energy efficient (i.e., when the participant believes the current trial is likely to contain an obstacle; Jax & Rosenbaum, 2007). However, the degree to which behaviours are fragmented within their hierarchal representation and the exact mechanism of how they predict an approximation of the best course of action on subsequent movements have yet to be elucidated (Barron et al., 2013; Haar & Donchin, 2020; McNamee & Wolpert, 2019).

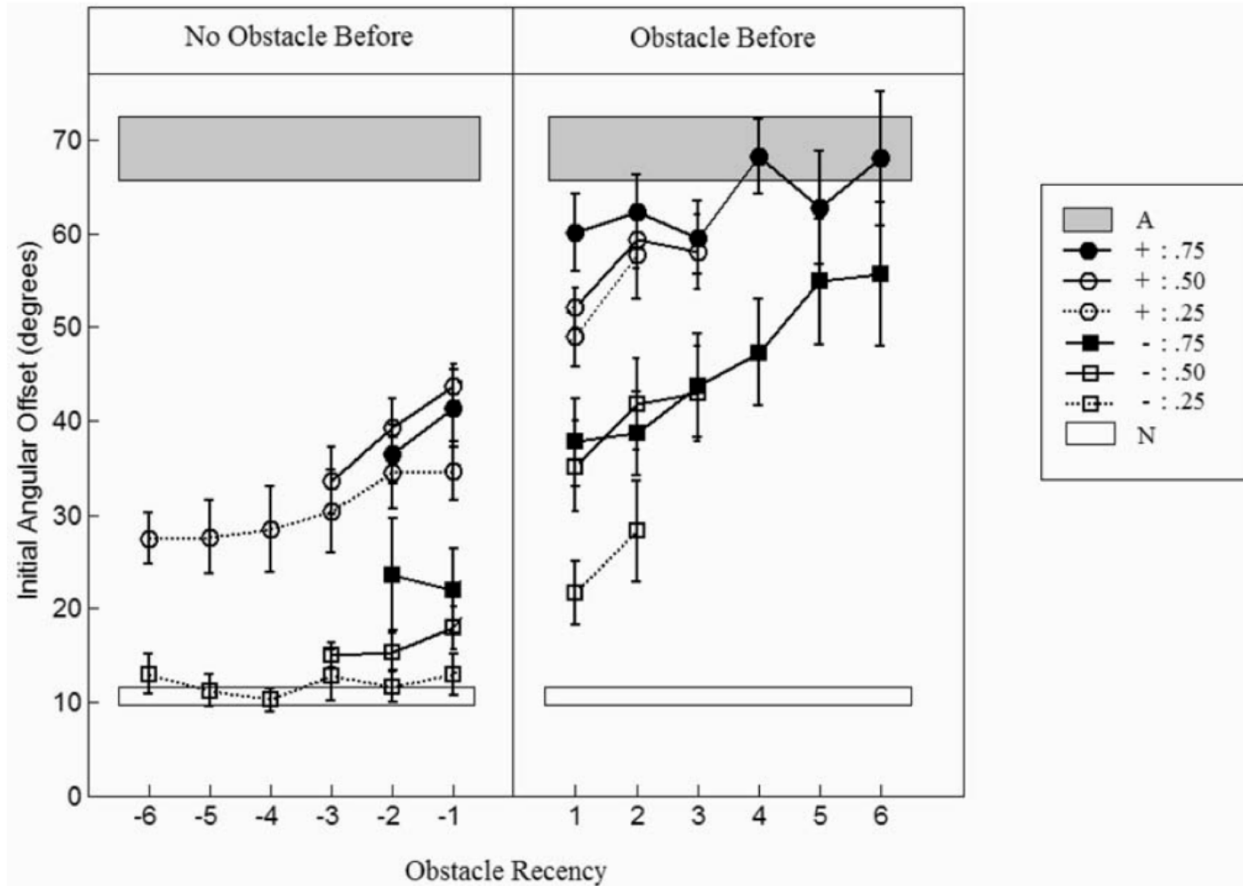


Figure 1.5: Results of Jax & Rosenbaum (2007) demonstrating hand path priming effects. This visualization shows the mean initial angular offsets ( $\pm 1$  SE) for reaches across conditions with differing likelihoods of an obstacle impeding the reach (range = 0[N] to 1[A]). The positive values on obstacle recency denote the number of consecutive preceding trials when an obstacle was present, and the negative values denote the number of consecutive preceding trials without an obstacle. The shape of each point denotes if an obstacle is present (circle) or absent (square) on the current trial. In the A and N conditions recency was not a meaningful factor and the rectangles denote the mean  $\pm 1$  SE across all levels of obstacle recency. Notably there was a significant interaction between obstacle recency, state of the current trial (obstacle vs. no obstacle) and likelihood of an obstacle trial being presented where the effect of obstacle recency was less noticeable in the 0.25 likelihood group in comparison to the 0.5 and 0.75 groups.

#### 1.4.2 Improving action execution:

In contrast to the process used to help improve goal and action selection, the process of improving action execution is much more implicit in nature and involves using sensory prediction error (see How do we execute movement) as a tuning signal to adapt to a changing environment or correct inaccurate motor commands as action is executed (Korenberg & Ghahramani, 2002; Martin et al., 1996; Mazzoni & Krakauer, 2006; Takahashi et al., 2001). This

process is indifferent to the reward or punishment generated by explicit knowledge of the task's outcome, indicated that it is governed by a separate process (Cashaback et al., 2017; Holland et al., 2018; Kooij et al., 2018, 2019). Given the biological noise present in sensory inputs to the brain, estimating the compensation contains a degree of uncertainty that can impair the accuracy of the compensatory signals (Korenberg & Ghahramani, 2002; Wei & Körding, 2009). This feature explains why no two movements are identical, even if the same goal and action are selected (Krakauer et al., 2019). Furthermore, along the lines of operant conditioning, high variability between movements in the early stages of motor learning increase the rate at which action execution is improved as a greater number of methods for executing a movement are explored. This early exploration of movements contributes to a broader understanding of the control policy that governs the movement and allows the most efficient movement to be more rapidly identified (Skinner, 1981; Wu et al., 2014).

It is the combination of the implicit process of improving action execution by monitoring sensory prediction errors and the more explicit strategies involved in goal and action selection operating in parallel that explain the typical exponential learning rate seen in adaptation paradigms (Huberdeau et al., 2015; Smith et al., 2006). These two components operate in different timescales where the early rapid improvement of task performance is thought to be reflective of improvements made to the explicit strategies used in action and goal selection and the later, slower performance improvements are governed by implicit advancements made during action execution (McDougle et al., 2015). While this evidence is generated on a trial-by-trial basis it is also reminiscent of the transition in autonomy across Fitts' laws which predicate

an early period of explicit cognitive control transitioning into implicit movement control in the autonomous stage of movement (Fitts & Posner, 1967).

### 1.5 *What is motor imagery:*

As introduced at the beginning of the last section, motor imagery is the mental rehearsal of movement without physical execution (Dickstein & Deutsch, 2007). Motor imagery has become of increasing interest due to its ability to drive motor learning in a variety of different applications including sequence learning, trajectory creation and aiming (Gentili et al., 2010; T. G. J. Ingram et al., 2019; W. Kim et al., 2014). Across both fundamental and applied research methods, motor imagery practice has largely demonstrated improvements in subsequent action execution, denoted by increased kinematic efficiency and accuracy of movement (Rienzo et al., 2016). While motor imagery is typically believed to be best employed as an adjunct to overt execution to maximize the rate of performance improvement, it has been demonstrated to be capable of driving motor learning independently of prior physical practice (Bovend'Eerd et al., 2012; S. N. Krautner, MacKenzie, et al., 2016; Zhang et al., 2011). However, common across many studies of motor learning via motor imagery is the finding that the degree of performance improvement due to motor imagery pales in comparison to physical practice (see How do we learn via motor imagery below; T. G. J. Ingram et al., 2019; T. Kim et al., 2017; Robin et al., 2007). These differences likely arise from the lack of feedback inherent to motor imagery and, as such, imagery practice must enable skill performance by different mechanisms. It has been therefore suggested that improved movement accuracy in motor imagery likely pertains to a better understanding of how movement is performed, governed by a control policy (T. Kim et al., 2017; S. N. Krautner, Keeler, et al., 2016). These behavioural differences in combination

with a high level of methodological variability used to study imagery contributed to an imperfect understanding of the mechanisms underlying the modality (Hurst & Boe, 2022; Ladda et al., 2021). A recent review of the prevailing motor imagery theories has been performed by Hurst and Boe (2022), many of which will be described briefly in the following sections.

#### *1.5.1 Motor simulation theory:*

The historical understanding of imagery was that it represents a subset of the process used in overt execution of a task (Jeannerod, 2001). Motor simulation theory suggests that imagery shares the same neural processes up until the initiation of movement and both modalities are functionally equivalent until the point of deviation, whereby action is executed in overt execution or inhibited in motor imagery (Jeannerod, 1994). The theory was originally evidenced by similarities in the mental chronometry between the two modalities and overlapping cortical representations (Burianová et al., 2013; Hardwick et al., 2018; Héту et al., 2013; Sirigu et al., 1995). However, despite the partially overlapping neural activity in the cortex, the claim of commonly used neural underpinnings between modalities raises questions as to the theory's accuracy due to notable differences in the cortical activation between modalities, especially in the parietal and motor cortices (Hardwick et al., 2018). Further, the inhibitory mechanism employed in motor imagery seems to be attached to the decision to engage in motor imagery rather than transiently inhibiting a motor command as the Bereitschaftspotential, a readiness potential for movement, commonly seen in the M1 is notably reduced or absent in motor imagery suggesting that motor imagery and overt execution engage different mechanisms during motor planning (Eagles et al., 2015; Shibasaki & Hallett, 2006; Solomon et al., 2019a).



### 1.5.2 *Motor emulation theory:*

At the highest level, motor emulation theory is a translation of optimal feedback control adapted to motor imagery in light of the lack of action execution (Grush, 2004; Todorov & Jordan, 2002). This theory is aligned with the previous motor simulation theory but has a more concrete mechanism to describe imagery (Grush, 2004). The fundamental mechanism in emulation theory is that imagery uses the forward modelling process employed during action execution to simulate movement and guide its subsequent adaptation (Krakauer & Mazzoni, 2011; Miall & Wolpert, 1996). Grush (2004) provides great detail to describe this emulation process as a Kalman filter, an algorithm that estimates the future state of the system and its corresponding uncertainty, further increasing its likeness to optimal feedback control that utilizes a similar Kalman filter to derive sensory prediction errors (Grush, 2004; Todorov, 2004; Todorov & Jordan, 2002). The primary difference between motor emulation theory and optimal feedback control is that the sensory prediction generated by the forward model cannot be compared to sensory afference during state estimation due to the lack of movement in imagery (Figure 1.3 state estimation). As such, the sensory prediction error used to guide movement is more-so a prediction error due to the lack of sensory information about movement, which has important implication for how learning can be realized in motor imagery (see section 1.6.1 The impact of forward models on motor imagery-based motor learning). This theory mirrors a hypothesis made in direct policy learning which suggests that sensory prediction errors are not calculated and, rather, sensory afference is compared directly to the goal of movement to adjust ongoing action execution. It is only in the absence or delay of sensory afference that a forward

model would be used to guide movement, as is the case in motor imagery (Hadjiosif et al., 2021; Todorov & Jordan, 2002).

A further important piece of evidence supporting motor emulation theory is the result that motor imagery engages forward models (Kilteni et al., 2018). In a somatosensory attenuation paradigm, it was found that motor imagery engages a forward model to attenuate the sensation of a self-touch in a manner similar to motor execution (Kilteni et al., 2018). Somatosensory attenuation is a phenomenon whereby the sensory outcome of a self-produced movement is diminished given that one actively predicts the sensory consequences of movement using a forward model (Blakemore et al., 2000). In the study conducted by Kilteni and colleagues, participants were asked to estimate the amount of force placed on their left index finger by a small direct current motor for three seconds which varied in magnitude (Figure 1.6 a-c). In the control condition participants placed their right hand beside the direct current motor apparatus and were asked to relax and remain at rest (Figure 1.6a). In the overt execution condition participants were asked to use their right index to replicate the force applied to the left index by the direct current motor on a transducer placed immediately above it, replicating the context of self-touch (Figure 1.6b). Lastly, in the imagery condition participants placed their right hand on the sensor and imagined replicating the force applied to the left index finger (Figure 1.6c). Immediately after the trial, the participants were asked to use a slider connected to the direct current motor to generate the matching force felt on the left index (Figure 1.6a-c). Interestingly, attenuation was seen in both the overt execution and the imagery condition in comparison to the baseline whereby reported forces were attenuated at all levels applied to the left index (Figure 1.6d). This was taken as evidence that imagery must be employing a forward

model as described in motor emulation theory to attenuate the externally provided force when it is perceived to be a self-generated touch (Figure 1.6e and f; Grush, 2004; Kilteni et al., 2018).

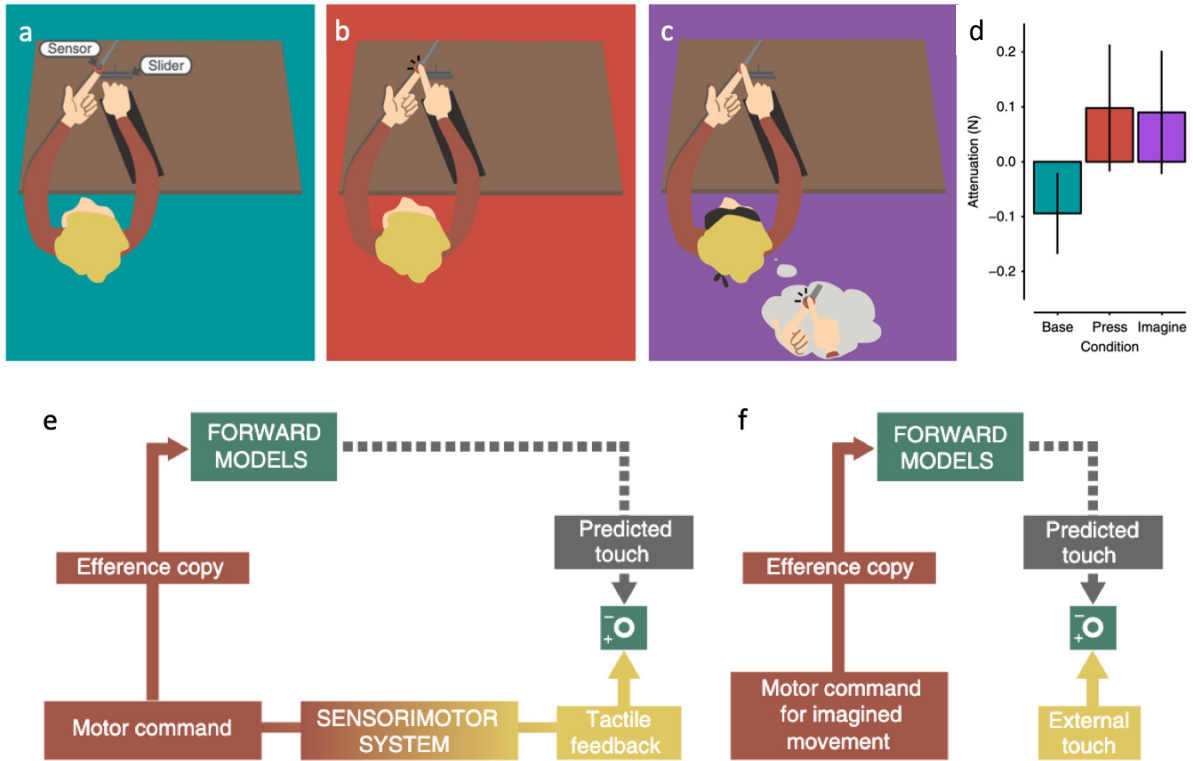


Figure 1.6: Select figures from Kilteni et al., (2018) modified for this visualization. Subplots a-c visualize the three experimental conditions where participants were asked to either remain at rest beside a direct current motor while it applied a force to their left index (control, subplot a), replicate that force on a sensor located otop of the direct current motor (overt execution, subplot b) or imagine replicating the force on the sensor over the direct current motor (motor imagery, subplot c). When subsequently asked to match the force applied to the left index using a slider (pictured in subplots a-c), participants attenuate the amount of force applied to their left finger in the overt execution and motor imagery conditions relative to the control group (subplot d). This mechanism is visualized as flow charts in Figures 6e, overt execution, and 6f, motor imagery, where the externally generated touch is used as a proxy for the sensory afference that would be created in overt execution.

### 1.5.3 Motor cognitive model:

In contrast to the previous two theories explaining the mechanism underlying motor imagery, the motor cognitive model presents a deviation from the architecture used to describe the control of movement in overt execution. After the creation of a control policy to govern

movement, the motor cognitive model suggests that motor imagery uses a separate cognitive pathway to create an internally maintained multi-sensory simulation of the movement (Glover & Baran, 2017). As a consequence of this decision, it was posited that if a control policy is not well understood it is a low fidelity movement and therefore more cognitively demanding than actions that are governed by a well-defined control policy or high-fidelity movement (Glover & Baran, 2017). Therefore, experimental tasks that increase the executive and attentional resources needed should be more difficult to perform via imagery than overt execution. The authors provide evidence of this theory from a behavioural study where participants were asked to count backwards while performing a reaching task resulting in increases to movement duration, estimated in motor imagery, that were larger in imagery in comparison to overt execution (Glover & Baran, 2017).

#### *1.5.4 Perceptual cognitive model:*

The perceptual cognitive model doesn't immediately conflict with the prior models for motor imagery however it does suggest a large change in focus whereby it postulates that imagery is reflective of the process of movement planning (Frank & Schack, 2017). This theory dictates that the experience of imagery is expressed through perceptual-cognitive reorganization. Perceptual-cognitive reorganization is the process of retrieving and efficiently organizing basic action components, kinematically simple movements and their associated sensory consequences, into a more elaborate hierarchal structure to represent complex movement (Frank & Schack, 2017). This theory was developed by the evaluation of expertise on motor tasks, whereby contrasting the hierarchal structure of movement in novice versus elite athletes revealed that athletes maintain a much more structured cognitive understanding of

movements in which they are experts (Schack, 2004; Schack & Mechsner, 2006). In a study of a golf swing, it was noted that both overt execution and motor imagery practice of the skill led to the development of a more complex cognitive structure of a golf swing, however, practice by overt execution led to better subsequent skill performance while imagery led to a more expert like cognitive representation of movement (Frank et al., 2013, 2014).

### *1.6 How do we learn via motor imagery:*

It is at this point that I would like to make an aside to denote a synergy between the study of motor control and theories of motor imagery. The development of motor simulation theory by Jeannerod in 2001 presented a significant development for the field of motor imagery but also served as a point of divergence whereby the study of imagery could become independent of overt execution. When motor simulation theory was formed, the prevailing belief of motor control was feedforward control of movement since optimal feedback control had yet to be introduced (C. M. Harris & Wolpert, 1998; Jeannerod, 2001; Todorov & Jordan, 2002). In the framework of feedforward control, it was widely believed that motor planning resulted in an exact kinematic/dynamic plan for movement that would be enacted as an ensemble. Therefore, when the idea of functional equivalence in motor imagery was proposed it likely had a feedforward representation of motor planning in mind, however, due to the vagueness of the mechanism proposed in motor simulation theory this observation is just speculation (Hurst & Boe, 2022; Jeannerod, 2001). When the motor control literature subsequently evolved to predicate that the outcome of motor planning is a control policy, a general rule for guiding the efficiency of a movement from any initial state of the effector and goal (see What is a motor plan), rather than an exact motor command, it was not explicitly

noted in the motor imagery literature. The recent proposal made by the perceptual cognitive model presents a surprising alignment of the motor imagery literature with the current understanding of motor control (Frank & Schack, 2017; McNamee & Wolpert, 2019). The perceptual-cognitive reorganization emphasized in the perceptual cognitive model is remarkably similar to the suggested formation of behavioural hierarchies currently being recognized in the motor control literature to suggest how a control policy can be updated while concurrently addressing the degrees-of-freedom problem (Frank & Schack, 2017; McNamee & Wolpert, 2019). The convergence of both streams of literature on this idea of building control policies that improve as a function of how well their hierarchal organization is understood provides a promising, parsimonious avenue to investigate a potential shared mechanism between motor imagery and overt execution to drive motor learning by improvements made in action selection through perceptual-cognitive reorganization. The finding that motor imagery leads to more accurately developed hierarchal representations of movement further highlights an important implication for motor imagery-based learning whereby attentional resources are not split across action selection and action execution as they are in overt execution (Frank & Schack, 2017; Hurst & Boe, 2022). In imagery attention is only allocated to processes involved in action selection which might contribute to the noted perceptual bias in motor imagery, bias towards covertly performed components of movement. This bias was noticed by the diverging effects of transfer amongst trained vs. untrained effectors and inhibitory TMS manipulations on behavioural motor learning tasks (see What is the cortical representation of motor imagery; Hurst & Boe, 2022; T. G. Ingram et al., 2016; S. N. Kraeutner, Keeler, et al., 2016; S. N. Kraeutner, Ingram, et al., 2017; Solomon et al., 2021).

### 1.6.1 *The impact of forward models on motor imagery-based motor learning:*

In addition to the improvements made to control policies as a function of motor imagery practice, evidence suggesting that motor imagery employs forward models indicates that the comparison of the predicted sensory consequences of movement to the movements goal could also be used to help drive learning in imagery (Grush, 2004; Hadjiosif et al., 2021; Kilteni et al., 2018; Todorov & Jordan, 2002). Stemming from this finding is the interesting observation that motor imagery performance can result in errors (Dahm & Rieger, 2019a, 2019b; T. G. J. Ingram et al., 2022). This result suggests that the forward model employed in imagery can predict mistakes and, therefore, drive motor learning through the provision of an error signal that represents a mismatch between the predicted sensory consequence of movement and the movements intention as governed by the control policy (Figure 1.7 upper right (X); Dahm & Rieger, 2019b). The question is, how does motor imagery predict a mistake? In overt execution, state estimation generates a sensory prediction error by comparing sensory afference to the predictions made by the forward model (Figure 1.3d; see How do we execute movement). However, in motor imagery there is no sensory afference. This observation served as the genesis for my first thesis chapter where it was postulated that motor imagery performance must also involve a simulation of sensory afference to generate an error. To evidence this decision TMS was used to transiently inhibit a brain region believed to be responsible for this function, the IPL (see section 1.7 What is the cortical representation of MI).

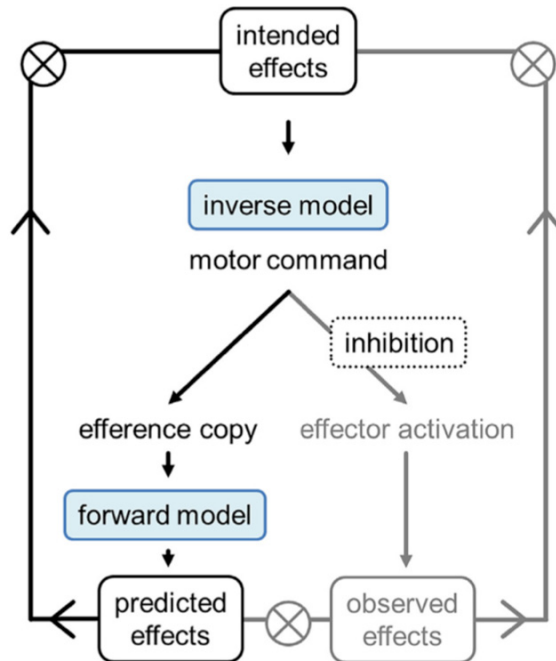


Figure 1.7: A computational framework for motor imagery taken from Dahm and Rieger (2019). In this framework for motor imagery the output of the forward model, the predicted sensory consequences of movement, can be compared against the intentions of movement as the only method to drive learning in the absence of sensory afference.

### 1.7 What is the cortical representation of motor imagery:

While the argument is presented earlier in this thesis that the understanding of cellular mechanisms is insufficient to explain behaviour due to a lack of context, the answers to which behavioural frameworks are most plausible can conversely arise from the underlying anatomy (Krakauer et al., 2017). With specific regards to the theories that define motor imagery, those aligning with the functional equivalency hypothesis (motor simulation theory and motor emulation theory) would suggest a high degree of overlap between the cortical representations of motor imagery and overt execution, in comparison to those suggesting alternative mechanisms for the two modalities (e.g., the motor cognitive model; Glover & Baran, 2017; Grush, 2004; Jeannerod, 2001). However, these representations need to be considered in the context of the primary behavioural difference between the imagery and overt execution, the



presence of movement. Specifically, the impact of lack of movement in motor imagery needs to be considered with reference to the recruitment of cortical regions involved in generating movement as well as the potential reallocation of cognitive resources towards behaviours that remain as part of the imagery experience, such as, perceptual-cognitive reorganization (Frank & Schack, 2017; Hurst & Boe, 2022). As such, even if the same cortical regions are recruited for a task, they may not be performing the same function (Poldrack, 2006). In addition to this ambiguity, there is also a methodological bias that needs to be considered, whereby tasks commonly selected in neuroimaging investigations of motor behaviours choose kinematically simple movements such that the head can remain stationary in the scanner (Hardwick et al., 2018; Puce & Hämäläinen, 2017). A consequence of this decision is that the neuroimaging accounts of motor imagery might bias the underlying networks to represent functions associated with goal and action selection due to the high-fidelity and kinematic simplicity of movements employed in these behavioural paradigms (Figure 1.2; Krakauer et al., 2019). It therefore remains a possibility that other loci of activity associated with more typical sensorimotor areas might be involved in motor imagery affecting conclusions surrounding the degree to which imagery relies on these covert components of movement (i.e., goal, and action selection). With both arguments in mind, mapping the areas involved in a behaviour can identify targets for further investigation to elucidate their role in behaviour.

A meta-analysis performed by Hardwick et al., (2018) of overt execution, denoted as motor execution in Figure 1.8, and motor imagery serves as the most updated reference for the cortical representations for each modality (see Figure 1.8a &b). Overt execution in this analysis revealed activity in the sensorimotor cortex, premotor cortices, IPL as well as subcortical

structures including the thalamus, putamen, and cerebellum (Figure 1.8a; Hardwick et al., 2018). Motor imagery recruited a more diverse collection of cortical structures including parts of the premotor cortex, the superior and inferior parietal lobes, cerebellum, basal ganglia, and the left dorsolateral prefrontal cortex (Figure 1.8b; Hardwick et al., 2018). The contrast of the two modalities revealed a bias of motor imagery towards greater recruitment of the parietal regions and selected premotor areas, whereas motor execution recruited more heavily from areas classically associated with the production of movement including the cerebellum, somatosensory cortex, supplementary motor area (SMA), and M1 (Figure 1.8c; Hardwick et al., 2018). The conjunction analysis comparing similarities between both modalities produced an overlapping activation of areas in the premotor cortex including the SMA, dorsal and ventral premotor cortices, somatosensory cortex as well as a small cluster in the cerebellum (Figure 1.8d; Hardwick et al., 2018).

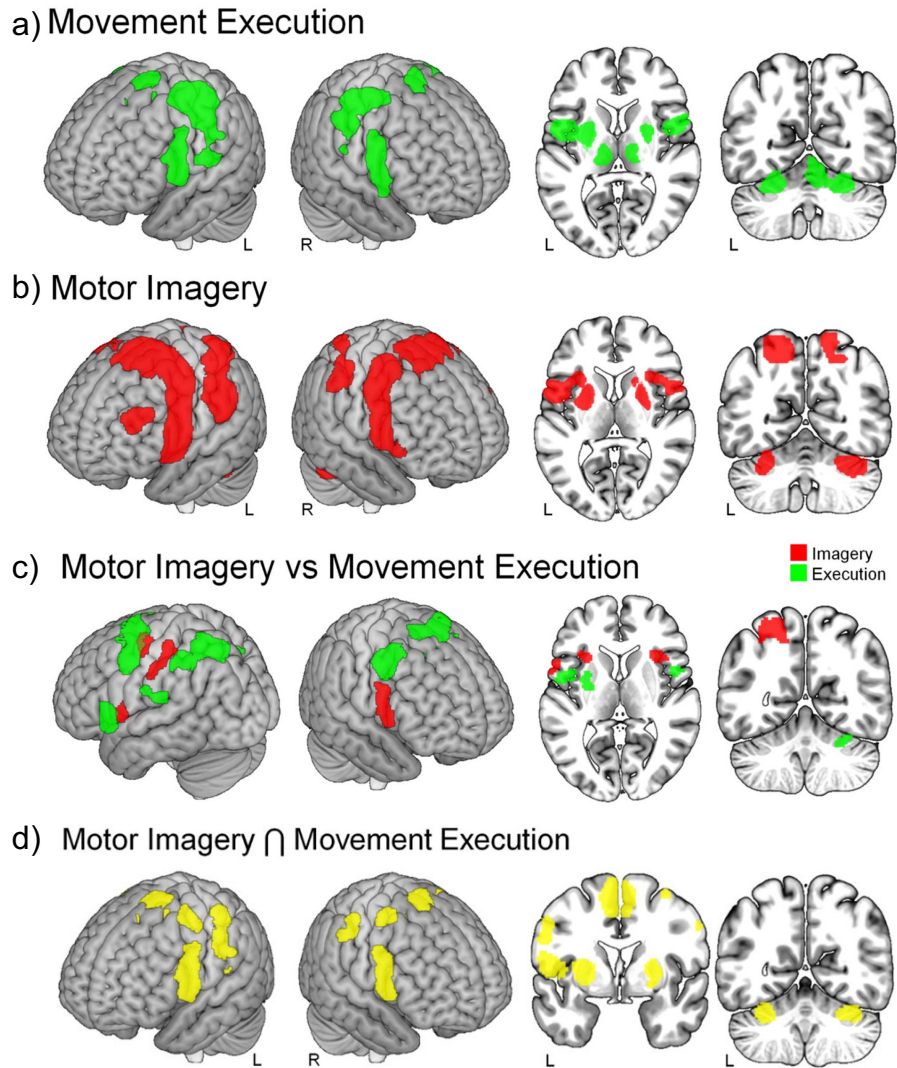


Figure 1.8: Results of an activation likelihood estimate meta-analysis of motor imagery in contrast and in conjunction with movement execution (overt execution) adapted from Hardwick et al., (2018). Subplots a and b denote the cortical regions active in 142 movement execution and 303 motor imagery studies respectively. Subplot c visualizes the cortical regions uniquely activated in motor imagery and movement execution respectively (motor imagery = red, movement execution = green). Subplot d shows the results of a conjunction analysis highlighting cortical regions activated during performance of movement in both modalities.

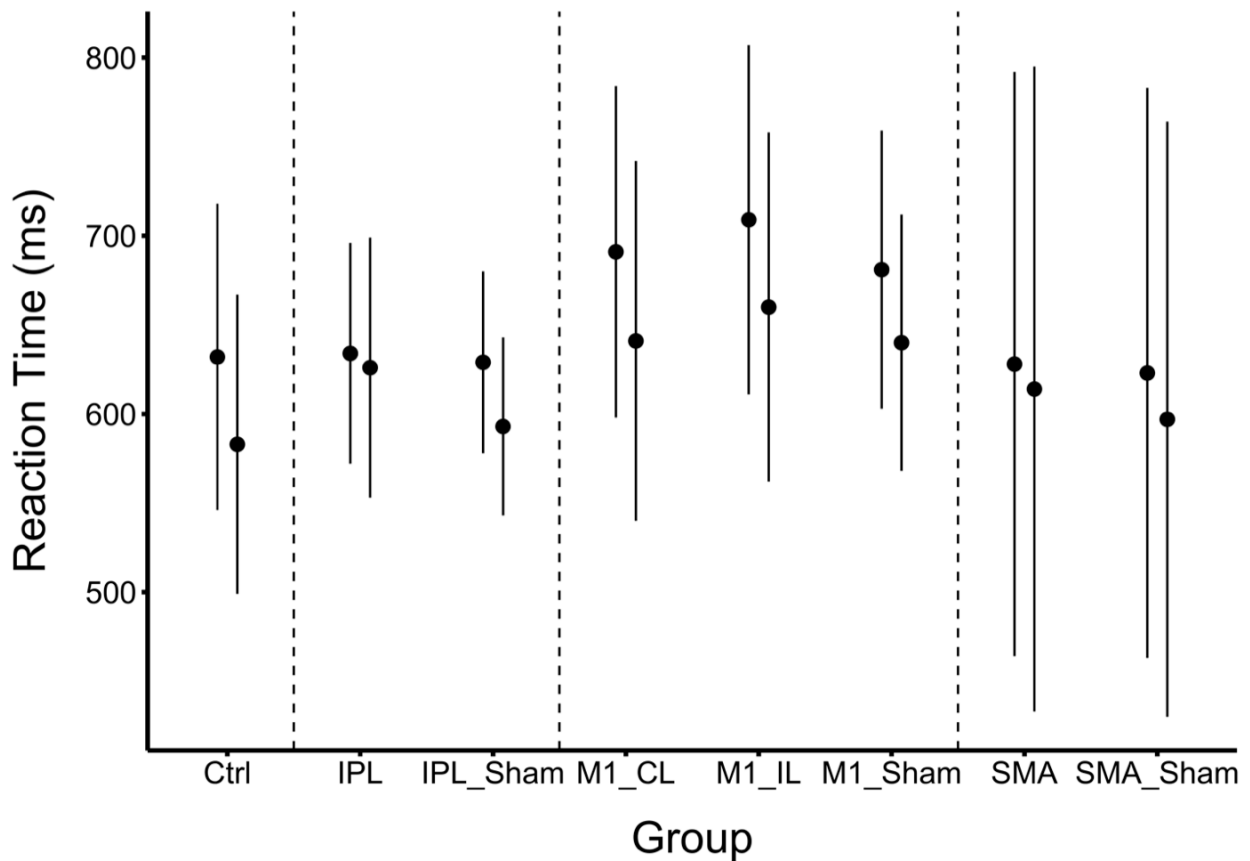
### 1.7.1 The importance of cortical regions to motor imagery-based motor learning:

From the analysis above, a few areas of the cortex become interesting targets for investigation, specifically the parietal regions that are recruited more heavily in motor imagery, the motor cortices that are recruited heavily in motor execution and the SMA that is jointly recruited by both modalities (Figure 1.8c&d; Hardwick et al., 2018). The motor cortices are

classically thought to be responsible for sending the final output of the brain to spinal motor neurons to begin movement, however, the area has also been implicated in the retention of learned motor skills (Grospretre et al., 2015; Richardson et al., 2006). The parietal lobes are commonly associated with a role of sensorimotor integration vital for interpreting visual information for movement via the dorsal visual pathway and are thought to be involved in the process of state estimation for motor control (Andersen & Buneo, 2002; Buneo & Andersen, 2006; Goodale & Milner, 1992; Haar & Donchin, 2020; Medendorp & Heed, 2019). Regarding state estimation, the IPL would incorporate sensory afference from movement with a sensory prediction from the forward model, commonly associated with cerebellar function, to generate the sensory prediction errors used to guide movement (Medendorp & Heed, 2019; Shadmehr & Krakauer, 2008; Sokolov et al., 2017). The SMA, an area active in both overt execution and motor imagery, is believed to be involved in several functions relating to action selection and timing of sequential movements (Cona & Semenza, 2017; Hoffstaedter et al., 2012; Lara et al., 2018). The area also seems to activate in response to upcoming sequences of previously acquired movements suggesting another possible role in the creation of motor chunks as a representation for a number of sequential actions (Tanji & Shima, 1994; Verwey et al., 2015).

To date, much of the research elucidating the functions of these areas came from inquiries about motor control completed using overt execution and, therefore, served as meaningful reference points to evaluate the neural mechanisms underlying motor imagery. From 2016 to 2021 our lab performed a series of studies examining motor learning via motor imagery using a serial reaction time task and selectively interfered with the function of the IPL, SMA and M1 using a type of repetitive TMS prior to training on the task (Huang et al., 2005; S.

N. Kraeutner, Keeler, et al., 2016; S. N. Kraeutner, MacKenzie, et al., 2016; S. N. Kraeutner, Ingram, et al., 2017; Solomon et al., 2021). In line with the contrast and conjunction analyses from Hardwick et al., (2018), stimulation to the IPL impaired sequence acquisition in motor imagery more than overt execution, stimulation to the SMA impaired sequence acquisition in both conditions and stimulation to the M1 impaired sequence acquisition more in overt execution than in motor imagery (Figure 1.9; (Hardwick et al., 2018; S. N. Kraeutner, Keeler, et al., 2016; S. N. Kraeutner, MacKenzie, et al., 2016; S. N. Kraeutner, Ingram, et al., 2017; Solomon et al., 2021). The results indicate motor learning via motor imagery relies on brain areas associated with mechanisms involved in goal and action selection, the IPL, and SMAs, but less so on the M1 which is associated with action execution.



*Figure 1.9: A summary of results from a motor imagery serial reaction time task [mean  $\pm$  SD] used in Kraeutner, Keeler, et al., (2016), Kraeutner, MacKenzie, et al., (2016), Kraeutner et al., (2017) and Solomon (2021). Prior to engaging in the experimental paradigm participants received real or sham repetitive transcranial magnetic stimulation delivered to the inferior parietal lobe, motor cortex or supplementary motor area. Note that that the mean values reported in all groups excluding the SMA and SMA\_Sham reflects the participant means, whereas values from the two SMA groups reflect every collected trial, hence the difference in variance.*

However, these conclusions came with two limitations. Firstly, due to the extended length of the inhibitory effect of the repetitive TMS (approximately 45-60 minutes), it was not possible to identify what the role for any of these cortical regions were. Rather, the findings denoted the relative importance of the regions to motor learning in either modality on the serial reaction time task. The second limitation was the task selection. While motor learning can be assessed using a wide variety of tasks, these tasks do not rely evenly on all mechanisms used to control movement (Figure 1.2; Krakauer et al., 2019). Specifically, serial reaction time tasks are a variety of sequence learning tasks that rely heavily on goal and action selection and very little on action execution which could have impacted the recruitment of cortical areas that are needed to complete the paradigm and created a bias in the results owing to the task used. These two factors served as further inspiration for my thesis whereby over the following chapters I sought to investigate two questions:

- 1) What is the role of the IPL in motor imagery?
- 2) Is task selection potentially biasing our view of the mechanisms underlying motor imagery?

### **1.8 Thesis chapter overview:**

This thesis aimed to address these questions by altering the approach used to transiently inhibit the brain such that a potential role for the IPL could be assessed, and by selecting a more complex behavioural task in which to evaluate learning. The task employed in

all the following chapters is a complex movement execution paradigm that according to the hierarchy presented in Figure 1.2 could be classified as de novo continuous learning (T. G. J. Ingram et al., 2019; Krakauer et al., 2019). While this progression of chapters was not as anticipated due to the COVID-19 pandemic and the role of the IPL was not adequately addressed, its results speak clearly to the effect of task selection in the study of motor imagery-based motor learning and improve our understanding of the neural correlates of motor imagery.

### *1.8.1 Chapter 2*

In the second chapter, we attempted to address both questions at once by employing a temporally discrete single pulse transcranial magnetic stimulation method to interfere with function of the L\_IPL after each bout of the complex movement execution task (Prime et al., 2008; Solomon et al., 2022). This approach was specifically designed to test if the region was involved in the provision of simulated sensory afference to permit state estimation (see How do we control movement). This study returned a null result and unfortunately its conclusion coincided with the onset of the COVID-19 pandemic. The null result forced a re-evaluation of the planned thesis projects, and the pandemic onset delayed the start of data collection for the subsequent chapters.

### *1.8.2 Chapter 3*

Since public health guidelines prevented data collection from continuing during the pandemic, we focused our attention on methodological improvements to the complex movement execution task. In collaboration with PhD student Austin Hurst, we improved the accuracy of our data analysis pipeline. During this process we identified the choice of outcome measure as a potential avenue for further improving the ability of the complex movement

execution task to detect changes in learning resulting from motor imagery training. Specifically, based on the belief that motor imagery helps improve action selection rather than action execution, the choice of mean error as an outcome measure for the behavioural task represented a bias towards action execution that could be masking the benefits of motor imagery training (T. Kim et al., 2017). As such, the third chapter set out to test a new correlation-based outcome measure to isolate improvements made to action selection on the paradigm by re-analyzing the data originally collected and reported in Ingram et al., (2019). The results indicate that the correlation-based outcome measure is able to detect changes in learning as a result of motor imagery and overt execution training and is indifferent to absolute spatial errors in action execution, supporting its use in subsequent studies.

### *1.8.3 Chapter 4*

At the onset of the pandemic the methods for the fourth chapter of this thesis, originally proposed as the third chapter, had just been piloted and data collection was set to begin. The study comprising the fourth chapter of the thesis aimed to solely address the impact of task selection on the contribution of cortical regions to motor imagery-based motor learning by replicating our lab's earlier results from the series of serial reaction time tasks on the newer complex movement execution paradigm (S. N. Kraeutner, Keeler, et al., 2016; S. N. Kraeutner, Ingram, et al., 2017; Solomon et al., 2021). This project used the correlation-based outcome measures developed in chapter 3 to characterize the effect of stimulation on action selection in an 8-group study differing on the brain region targeted by the stimulation (L\_IPL, SMA, M1 and SHAM) and practice modality (motor imagery and overt execution). Rather than using the single pulse stimulation paradigm employed in chapter 2, a time insensitive repetitive TMS paradigm



was used to induce a virtual lesion prior to training on the complex movement execution task. Results of this study denoted the importance of the L\_IPL to motor imagery-based motor learning as inhibitory stimulation to this brain region impaired learning on the task. However, Results from the M1 and SMA stimulation did not align with the prior literature. The lack of consistent findings highlights the limitations of the current stimulation-deficit design when applied to single tasks. From these results we suggest that interpretation of the findings from such studies need to be limited or future studies should use a battery of behavioural tasks to overcome the limitation noted above.

#### *1.8.4 Contributions to Thesis Chapters:*

Chapters one and five of this thesis are written by Jack Solomon and edited in collaboration with Dr. Shaun Boe.

Chapter two reports a project devised by Jack Solomon and Dr. Shaun Boe. Data collection and analysis was completed by Jack Solomon under the supervision of Dr. Shaun Boe with the aid of JungWoo Lee (data collection) and Austin Hurst (data analysis). Jack Solomon wrote the initial draft of the manuscript with editing and revisions completed in collaboration with Dr. Shaun Boe.

Chapter three reports a re-analysis of data collected and reported in Ingram et al., (2019). The original project was conceived by Drs. Tony Ingram, David Westwood, and Shaun Boe. The novel analysis was conceived and implemented by Jack Solomon and Austin Hurst. The chapter was written by Jack Solomon with editing and revisions completed in collaboration with Dr. Shaun Boe.

Chapter four reports a project that was conceived by Jack Solomon and Dr. Shaun Boe. Data collection was led by Jack Solomon under the supervision of Dr Shaun Boe and was aided primarily by Taylor Hadskis, Darby Green, and Hannah Lee. Data analysis and manuscript writing was completed by Jack Solomon with editing and revisions completed in collaboration with Dr. Shaun Boe.

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## CHAPTER 2: ARE OBSERVED EFFECTS OF MOVEMENT SIMULATED DURING MOTOR IMAGERY PERFORMANCE?

A version of this chapter has been published.

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### 2.1 *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.

## 2.2 *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 2.1A 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).

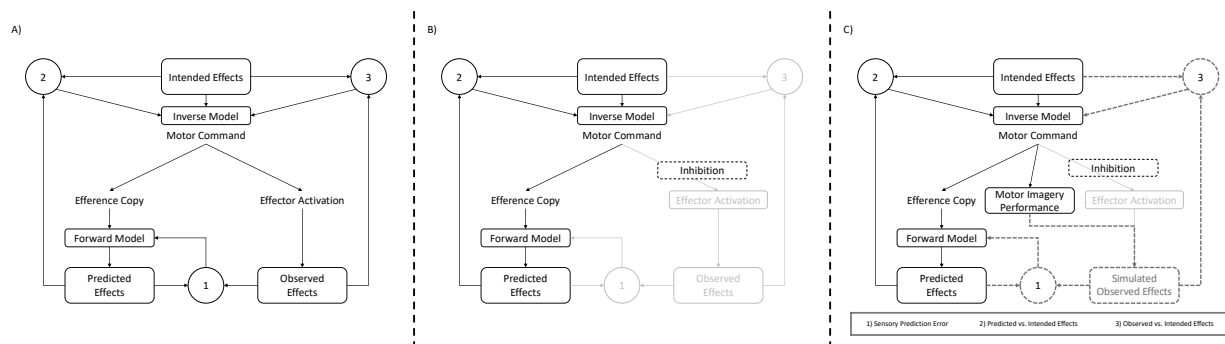


Figure 2.1: A) Framework for motor learning occurring via overt movement, adapted from Blakemore et al., (2002); briefly, as a motor command is sent to the effectors, the efference copy is used as input to a forward model. The forward model serves to predict the upcoming state of the effectors (predicted 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 Dahm and Rieger, (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 (T. G. J. Ingram et al., 2019; T. 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 2.1B; see circle 1). Nor could the observed effect of movement be used as a comparator to the intended effect (Figure 2.1B; 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 2.1B; 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 motor imagery 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 bullseye" 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 (T. G. J. 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 2.1B, 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 2.1B 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. Thus the error arising from the comparison of the predicted to intended effect would indicate that adjustments should be made to future attempts at movement (Figure 2.1B, 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 2.1C; 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 2.1C; 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 2.1C). In overt movement, the process of updating a forward model is attributed predominantly to

three regions of the brain: the motor cortex (M1), the parietal lobe, and the cerebellum (Desmurget et al., 1999; Popa & Ebner, 2019; Schieber & Poliakov, 1997; Shadmehr & Krakauer, 2008). The M1 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 stroke patients to perform motor imagery (as assessed via motor imagery ability questionnaires) 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 2.1C; Burianová et al., 2013; Hardwick et al., 2018; Héту 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 (S. N. Kraeutner, Keeler, 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 2.1C). 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 transcranial magnetic stimulation (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 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 2.1C; 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 2.1C; 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.

## 2.3 *Methodology:*

### 2.3.1 *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  $22.4 \pm 3.5$  (mean  $\pm$  SD) 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 ( $22.5 \pm 3.1$  and  $22.2 \pm 3.9$  years for the stim and sham groups respectively) and imagery ability in the kinesthetic domain (KVIQ kinesthetic scores:  $20.8 \pm 3.4$  and  $21.5 \pm 3.1$  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.

### 2.3.2 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 (T. G. J. 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 2.2). 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 2.3).

### 2.3.3 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 2.2). 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.

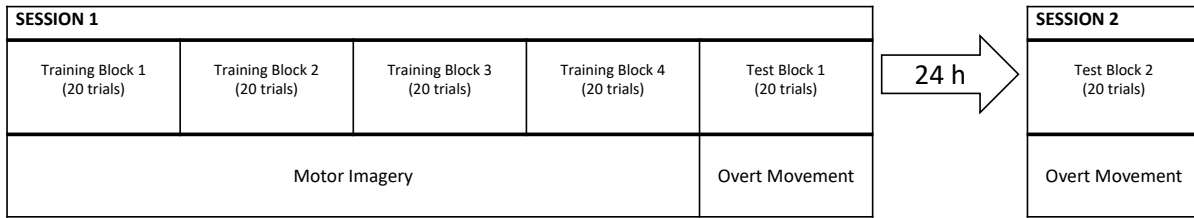


Figure 2.2: Experimental timeline. Following informed consent, screening and questionnaires, participants completed 4 blocks of training via motor imagery, receiving TMS 100ms after each trial to the L\_IPL (stim group) or over the vertex of the head (sham group), followed by a test block of 20 trials 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.

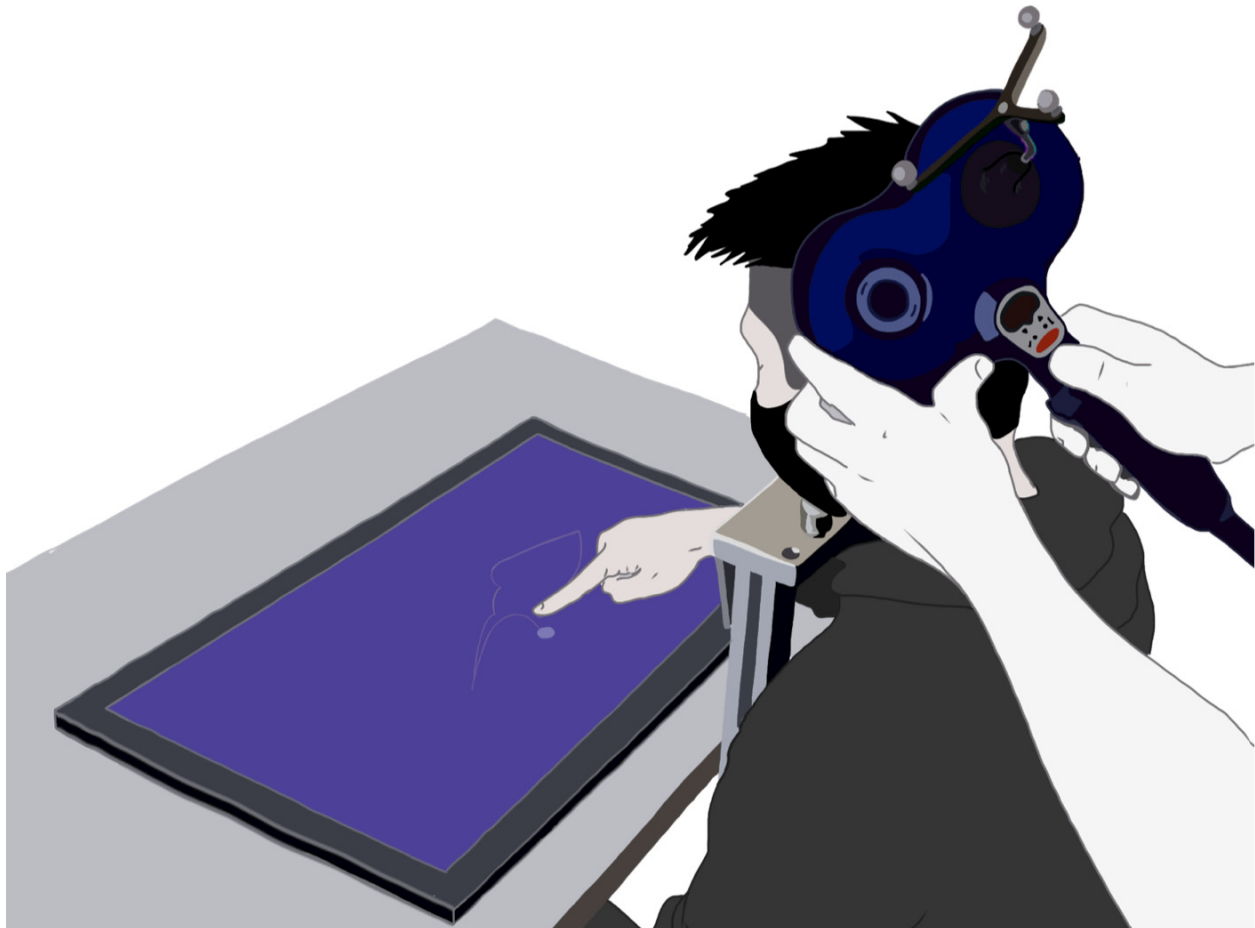


Figure 2.3: Experimental set-up. Participants reproduced complex trajectories via motor imagery (practice trials) and overt movement (assessment) on a touchscreen monitor. Inhibitory brain stimulation was delivered via transcranial magnetic stimulation over the L\_IPL (stim group only). Overt movement trial shown to demonstrate an example trajectory. Note: trajectory shown for illustrative purposes only; feedback was not provided to participants during overt movement trials.



#### 2.3.4 *Transcranial Magnetic Stimulation:*

Neuro-navigated TMS was performed using a BiStim<sup>2</sup> magnetic stimulator via a 70-mm figure of eight coil (Magstim, Whitland, UK) coupled with aBrainsight<sup>TM</sup> system (Rogue Research Inc., Montreal, Canada). For neuro-navigation, each participant's head was co-registered to a template magnetic resonance image (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 L\_IPL (-36, -23, 34 [X, Y, Z]; MNI space; S. N. Kraeutner, Keeler, 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 2.3), 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). The intensity and timing of the stimulator output was informed by the protocol used by Prime et al., (2008) who applied a similar single pulse paradigm targeting the IPL, which noted an effect of stimulation on behaviour.

#### 2.3.5 *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 2.2.

### 2.3.6 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  $>90^\circ$  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  $>120^\circ$  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.

### 2.3.7 *Statistical Analysis:*

Bayesian linear mixed-effects regressions were used to make statistical inferences regarding group performance on the task across study sessions. A linear mixed-effects model was selected over the more traditional analysis of variance to leverage the statistical power of the full dataset and characterize inter-participant differences (i.e., differing levels of performance [random intercepts] as well as different rates of skill acquisition [random slopes]). 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 posterior 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  $\pm$  standard deviation throughout.

#### 2.3.8 *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, 2023) and the packages *tidyverse* version 1.3.1 (Wickham, 2014), *vegan* 2.5-7, *TSEntropies* 0.9, *brms* 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.

## 2.4 Results:

### 2.4.1 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 2.4). 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 2.4; T. G. J. 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 2.4).

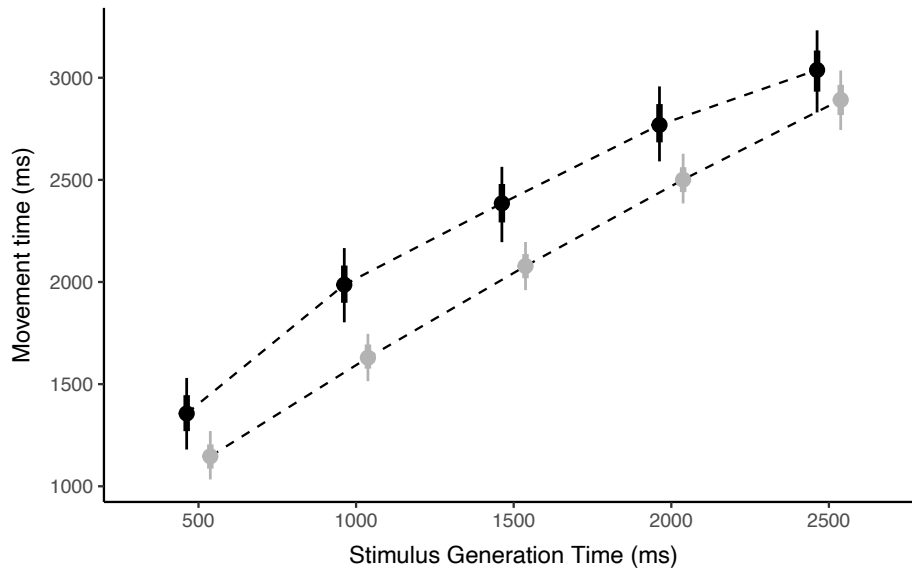


Figure 2.4. Scatter plot of participants' movement times at different stimulus durations in each modality (black: motor imagery; grey: overt movement) after controlling for within participant effects. Thick vertical bars indicate 60% HDPIs and thin vertical bars indicate 90% HPDIs.

#### 2.4.2 Error:

Error on the random and repeated trajectories in the sham group was  $96.0 \pm 38.2$ px and  $92.2 \pm 26.4$ px in session one and  $101.6 \pm 47.4$ px and  $91.4 \pm 25.4$ px in session two. For the stim group, error on the random and repeated trajectories was  $96.1 \pm 32.3$ px and  $89.8 \pm 21.5$ px in session one and  $100.3 \pm 39.0$ px and  $88.5 \pm 24.5$ px in session two (Table 2.1, Figure 2.5A). 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  $94.7 \pm 7.2$ px and  $85.4 \pm 6.2$ px (mean  $\pm$  90% HPDI) and  $95.6 \pm 9.2$ px and  $85.8 \pm 8.0$ px (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  $93.6 \pm 7.0$ px and  $84.6 \pm 6.5$ px in session one and  $94.1 \pm 9.4$ px and  $85.1 \pm 7.8$ px in session two (Table 2.1, Figure 2.5B).

Table 2.1. Mean trajectory error calculated from the observations (mean  $\pm$  SD) and drawn from the posterior distribution of the Bayesian model, and error controlling for animation velocity and trajectory complexity (mean  $\pm$  90% HDPI) for each group separated by trial type.

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

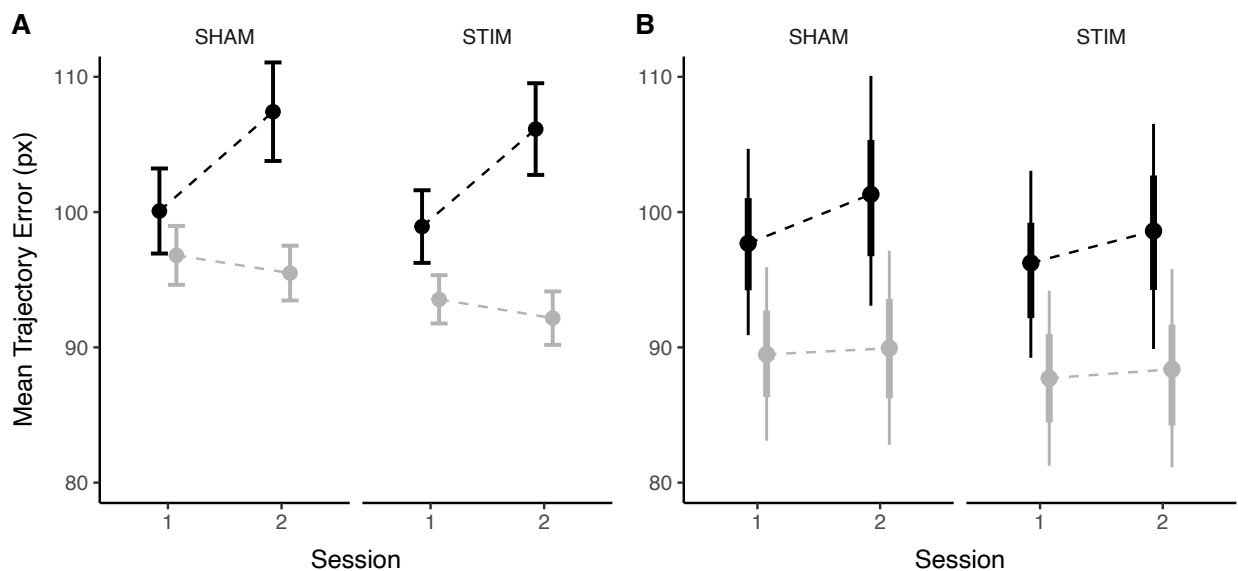


Figure 2.5. A) Scatter plot of the effects of figure type (black: random; grey: repeated) within the Sham and Stim groups across both experimental sessions on raw error. Vertical bars indicate standard error. B) Scatter plot of the effects of figure type (black: random; grey: repeated) within the Sham 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 2.6A-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 =  $\sim 1$ , 90% HPDI: 0.20 to 0.12, ROPE Percentage =  $5.0 \times 10^{-5}$ , Figure 2.6A). The effects of both animation velocity and trajectory complexity indicate that participants had a greater difficulty producing the stimulus trajectories as the stimulus animation velocity increases (MPE:  $\sim 1$ , 90% HPDI: 0.65 to 0.46, ROPE Percentage = 0, Figure 2.6B) and as the stimulus becomes increasingly complex (MPE:  $\sim 1$ , 90% HPDI: 0.21 to 0.06, ROPE Percentage = 0.19, Figure 2.6C). 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  $7.34 \times 10^{-3}$ , ROPE Percentage = 0.67), 2) session X trajectory complexity (MPE= 0.96, 90% HPDI: 0.15 to  $3.38 \times 10^{-3}$ , 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:  $3.81 \times 10^{-3}$  to -0.17, ROPE Percentage = 0.58).



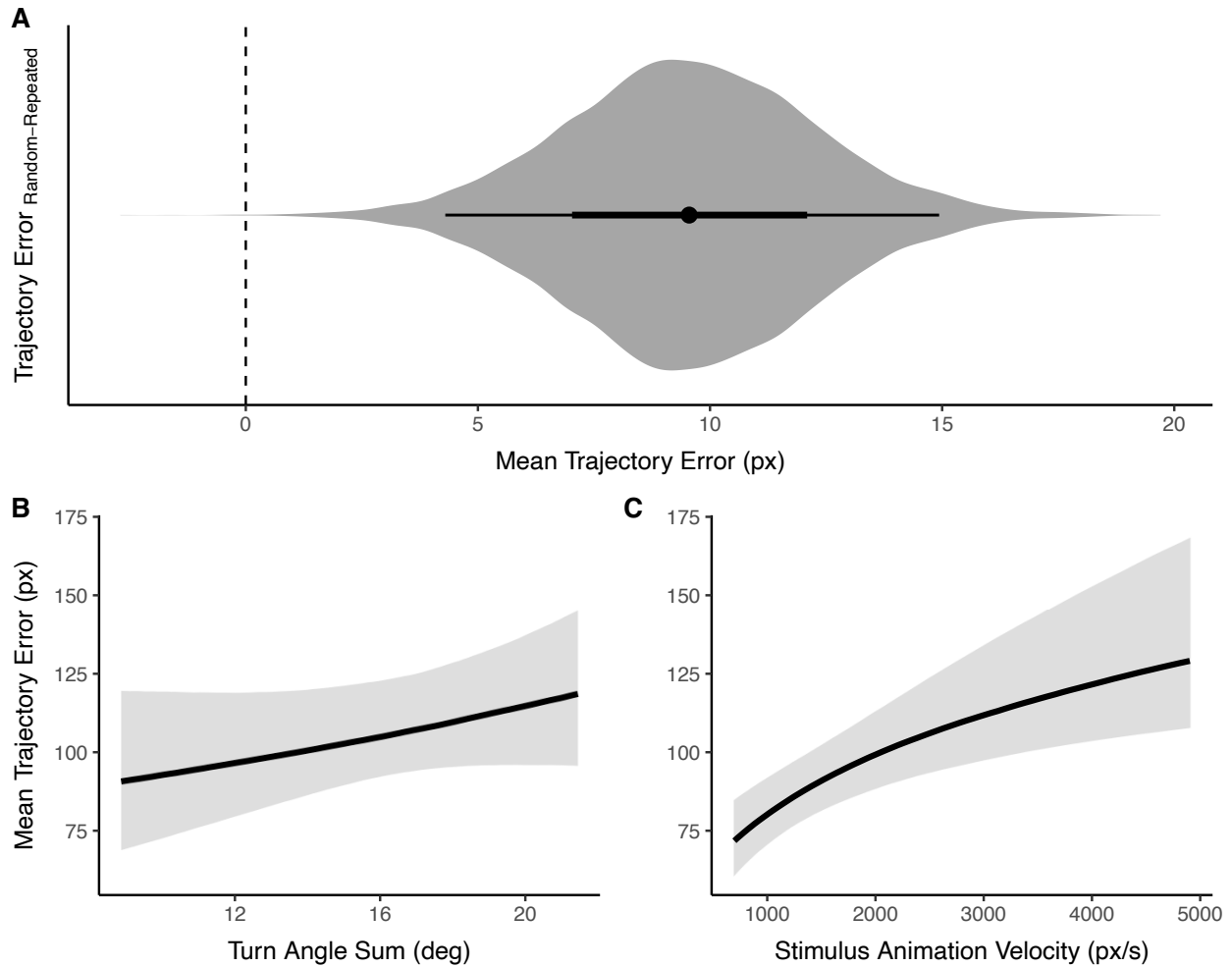


Figure 2.6. A) The distribution (grey shaded area) of differences between trajectory error on random and repeated trajectories controlling for all other predictor variables. The thick horizontal bar indicates 60% HDPIs and thin horizontal bar indicates 90% HDPIs. B) The effect of animation velocity on 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).

## 2.5 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 2.1C, 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 previous findings (T. G. J. 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 (T. G. J. 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. Four 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 2.1B). Secondly, the L\_IPL is not involved in the process of generating simulated observed effects of movement for comparison against its intended effect (Figure 2.1C, see circle 3). Thirdly, there could be incongruency between the proposed function of the L\_IPL and the timing of the stimulation that was intended to interrupt it. Finally, the stimulation could have been ineffective in that it did not have the desired inhibitory effect.

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 section 2.2 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 M1 via the dentatohalamocortical pathway and has been reported as being active during motor imagery 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 M1 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 2.1C, 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, its dense connections with frontal regions of the brain including the premotor cortices, its 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 motor imagery (Andersen & Buneo, 2002; Fogassi et al., 2005; Fogassi & Luppino, 2005; Hardwick et al., 2018; Héту 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 (S. N. Kraeutner, Keeler, 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 (I. M. 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 limitations were the timing of the single-pulse TMS and the lack of a control condition. To ensure that the single pulse stimulation was interfering with function of the L\_IPL, the original paradigm from Prime et al., (2008) would have needed to be replicated. As such, it is possible that the stimulation in this study did not produce the desired effect on the cortex, leading to the null result. Additionally, 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 2.1C, 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-supplementary motor area 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 100ms 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 2.1C, 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.

## *2.6 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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## Chapter 3: ESTABLISHING AN OUTCOME MEASURE REPRESENTING THE QUALITY OF A MOTOR PLAN

### 3.1 *Abstract:*

Motor skills are learned through two processes: a faster explicit process of identifying the movement to be performed, action selection, and a slower implicit process that represents improvements in movement acuity, action execution. In motor imagery these improvements are thought to be driven by changes to the perceptual understanding of the task, improving action selection. In contrast to this hypothesis most motor learning studies use an outcome of action execution, error, to assess the quality of task performance. However, action execution is notably absent in motor imagery and therefore this study sought to establish a measure of performance that was more indicative of action selection. Specifically, correlations were explored to measure the similarity between stimulus and participant response as they are unaffected by the absolute distance between the two and are therefore less reflective of inaccuracies in action execution. This study re-analyzed data from Ingram et al., (2019) using an updated data analysis pipeline to investigate the potential use of a correlation-based outcome measure. Results of this study overcome several limitations of the original analysis while minimally affecting the quantitative conclusions drawn from the statistical model. Additionally, the correlation-based outcome measure demonstrated a meaningful improvement resulting from imagery training on the complex movement execution task relative to the perceptual control group and serves as a promising approach to evaluating the accuracy of the control policy used to govern movement in future applications of this task.

### 3.2 *Introduction:*

Recent interpretations of motor imagery, the mental rehearsal of movement, have highlighted a bias of the modality towards using improvements to the accuracy of the control policy governing movement to drive motor learning through improvements in action selection (Frank & Schack, 2017; Hardwick et al., 2018; S. N. Kraeutner, Keeler, et al., 2016; Krakauer et al., 2019; Todorov & Jordan, 2002). The control policy is a rule which takes the form of a Bellman equation that balances the energy expenditure required to move against the accuracy of movement to emphasize the efficiency of movement in obtaining an accurate result (McNamee & Wolpert, 2019). However, due to the degrees-of-freedom problem, it is extremely slow to learn these policies through simple trial and error (Bernstein, 1967). Instead, it is suggested that smaller elements of movements known to the learner are grouped together to create a motor chunk. A motor chunk then is a singular representation for a sequence of these simpler movements that reduces the number of constructs needed to understand and learn complex movement (McNamee & Wolpert, 2019; Schack, 2004; Schack & Mechsner, 2006; Verwey et al., 2015). Learning motor skills is generally believed to be governed by this rapid, more explicit process of identifying what movement is to be performed and a slower, implicit process that represents improvements to movement acuity (Martin et al., 1996; Taylor & Ivry, 2011). In motor imagery, learning can be derived from two signals: a forward modelling process that predicts the position of the effector's imagined performance, and a reward prediction error that encodes the outcome of the imagined movement (Dahm & Rieger, 2019b; Kiltner et al., 2018). Despite the lack of movement in motor imagery evidence suggests that the outcome of an Imagined movement is encoded as motor imagery can result in self-reported error, a reward



prediction error, that could be used to drive adaptation (Dahm & Rieger, 2019b, 2019a; T. G. J. Ingram et al., 2022; McNamee & Wolpert, 2019). The combination of a reward prediction error and evidence of improved perceptual-cognitive reorganization contributes to the understanding that motor imagery emphasizes the perceptual processes involved in action selection over its subsequent execution (Frank & Schack, 2017; Hurst & Boe, 2022). This perceptual bias in motor imagery has been reinforced by behavioural evidence identifying the resilience of learned skills via motor imagery to effector transfer tasks, the reliance of the modality on the parietal lobes, and a notable lack of involvement of the motor cortex (M1) in the network underlying motor imagery performance (T. G. Ingram et al., 2016; S. N. Kraeutner, Keeler, et al., 2016; S. N. Kraeutner, Ingram, et al., 2017). However, the outcome measures commonly used to assess motor learning are largely based on metrics that result from overt execution of a skill, an aspect of movement that is by definition absent in motor imagery.

Paradigms used to investigate motor learning often examine outcome measures associated with the magnitude of errors or consistency of responses when assessing improvement on a motor skill. Frequently used measures are: physical distance of an effector or object from a goal (i.e. the final position of a dart from the bullseye or the distance of a finger from a goal box), the consistency of responses (i.e. grouping of the end position of golf balls after putting), kinematic proximity to an optimal movement (i.e. deviations from an optimal reaching trajectory), or dynamic proximity to an optimal movement (i.e. lifting or grasping tasks) (Buckingham et al., 2016; Dahm & Rieger, 2019b; Frank et al., 2013; Nashed et al., 2012). These measures are logical choices for analyzing improvements in performance on a motor task and are often considered 'gold standards' for assessing motor learning. However, when learning is

achieved through motor imagery, where physical execution of the skill is not practiced, it is worthwhile to explore if alternative measures can be used to represent the more explicit cognitive strategies used to help select which actions to perform (Krakauer et al., 2019). In the motor imagery literature, attempts have been made to quantify the improvements made to motor planning processes emphasized during imagery training, notably through clustering analyses of basic action components (Frank et al., 2014). The clustering analyses employed in the study of imagery have been used to create dendrograms of basic action components. By comparing dendrograms before and after training the organization of movement can be quantified by identifying the number of significant clusters and their size (Schack, 2004). In this analysis, the greater number of correct clusters and the larger size of each cluster, the more organized the practiced movement is.

In the complex movement execution task employed in this study (described in detail in chapters 2,4 and in the methods below) the outcome measure used in all publications to date has been error, a derivative of the distance between the participants responses and the stimuli. In this task the recorded data are pixel location of either the cursor (stimulus) or participant's finger (response) sampled at 60Hz (T. G. J. Ingram et al., 2019). Two steps have been included in the analysis of this data in an attempt to account for variability in the speed of participant responses and the orientation of the response relative to the stimuli: dynamic time warping (DTW) and Procrustes analysis (Giorgino, 2009; Goodall, 1991). Dynamic time warping was used to account for the variability in the speed of participant responses by minimizing the distance between samples of the participants response and the samples from the corresponding stimuli (Giorgino, 2009). Critically, DTW uses a step pattern which describes which possible pairing of

finger and cursor positions can be evaluated to minimize the error across the whole trial (Mori et al., 2006). The effect of this step was most noticeable in the 'corners' (where the stimulus abruptly changes direction) of a response where participants slow down their movement, clustering points around the change of direction despite the stimulus they are reproducing being animated at a constant speed. Once DTW is applied, the response is then rotated, translated, and scaled to best align it with the stimulus using a Procrustes analysis (Goodall, 1991). This step was an attempt to correct for errors related to the execution of the selected action. This analysis was used by Ingram et al., (2019) to demonstrate that motor imagery can lead to better learning of a novel complex motor task in comparison to a perceptual control group. Despite the efforts made to correct for variable participant response speeds and execution mistakes, the outcome measure of the task is still reliant on the participant's ability to accurately execute the drawn trajectory, a skill noticeably not practiced in motor imagery training. In short, the analysis applied to this complex motor task may not be reflective of what a participant is learning via motor imagery, namely improvements in motor planning.

The purpose of this re-analysis of data was twofold: 1) to provide improved control over the variability in the speed of participant's responses and 2) to establish an outcome measure that is a better representation of the control policy generated during action selection. To achieve this end, the data collected in Ingram et al., (2019) was re-analyzed using novel methodology to compute the correlation in turn angles between the participant response and corresponding stimuli. In this updated analysis an additional interpolation step is introduced to account for variance in the speed of participant responses before the turn angles are calculated and used to guide DTW. Finally, the Procrustes transformations are applied to the participant

response to minimize the distance between stimulus and response trajectories. By comparing the error attained from the end of this analysis to the analysis applied in Ingram et al., (2019), the inter-group differences should be consistent when the same Bayesian linear mixed model is applied with a term for the analyses used. The study's second purpose was to create an outcome measure that is resilient to errors in action execution such that it better reflects improvements made to action selection. With the current dataset, it would not be possible to apply a clustering analysis akin to methodology used in Frank et al., (2013) so instead we explore the possibility of measuring the similarity between the turn angles of stimulus and response trajectories using a correlation-based measure. Validation of this correlative-based measure would be evident in its ability to highlight the improvements in skill execution after a period of imagery training in comparison to engagement in a perceptual control task.

### **3.3 Methodology:**

#### **3.3.1 Dataset:**

Sixty-six participants completed training for 5 sessions over 5 days on a trajectory task where each session was comprised of 5 blocks of 20 trials. At trial onset participants were pseudo-randomized into one of four conditions indicating the modality and level of feedback they were to receive during training. Two groups performed the task physically: one received feedback regarding their performance after each trial (physical practice feedback, PPFB) while the other did not (physical practice, PP). The third group performed the task using first person kinaesthetic motor imagery (MI) in the first four sessions and then responded physically in session 5. The last group served as a perceptual control (PC) whereby they simply attended to the stimuli and responded to a question during the first four sessions (description below in

section 3.3.2 Task) and then responded physically during session 5. The data used in this analysis pertains solely to overt execution of the task, the relationship of the stimulus to participant responses when present, and the analysis of movement time and perceptual control tasks are not addressed. This left data from all 5 sessions for the PP and PPFB groups and data from the fifth session for the MI and PC groups.

### 3.3.2 *Task:*

The complex movement execution task is described in detail in Ingram et al., (2019). Briefly, trials consist of two phases: stimulus presentation and participant response. During the stimulus presentation a white dot traces out a series of 5 Bezier curves on a touchscreen in a clockwise direction. Each trajectory is closed such that the fifth Bezier curve ends where the first one began. The trajectories animate at one of five durations (ranging from 500-2500ms) such that there was an equal exposure to all durations across each block of the experiment. Additionally, one stimulus was presented repeatedly to each participant over the course of their training ('repeated trajectory', the trajectory to be learned), such that they saw the repeated trajectory in 50% of trials and random trajectories the other 50%. Random trajectory stimuli were generated at the onset of the trial. The presentation of the repeated trajectory was also randomized across the experiment with the constraint that they saw an equal number of the repeated and random trajectories within each block.

The subsequent participant response phase of each trial differed depending on group allocation. In the MI, PP and PPFB groups, the start of this phase was denoted by a red circle appearing on the screen as a start point. Participants then pressed on the start point circle, whereby it turned green and then either physically traced the stimulus trajectory matching the

speed of the animation (PP and PPFB) or imagined doing so (MI). When the participant returned their hand to the start point circle (PP and PPFB) or lifted their finger when they were done imagining their movement (MI) the start point circle would disappear and the trial would end. The PPFB group would then be shown an image overlapping their response on the stimulus trajectory to guide their learning, whereas the other groups received no feedback. In the PC group, rather than responding by re-creating the trajectory, participants counted the number of times the cursor bounced in a given direction during the presentation of the stimulus. During the participant response phase they would provide an answer to this query.

### *3.3.3 Analysis:*

In the original article, the analysis process for the participant responses contained 3 steps to ascertain the error, Euclidean distance (px), between cursor and finger locations in the stimulus and participant responses respectively. Firstly, responses or stimuli were down sampled to the length of the shortest vector to facilitate a simple point by point comparison. Subsequently, the resulting vectors were subjected to DTW to correct for variations in the participant responses. This was completed using a step pattern, symmetric2, that allows for points from both the stimulus and response to be endlessly repeated in order to minimize the error on a given trial (Giorgino, 2009). Finally, a Procrustes analysis was applied to rotate, transform, and scale the participant response such that they align with the stimulus to again minimize the error between both trajectories. The current analysis uses similar tools however reassigns the purpose of each analytical step to differing goals. Rather than using DTW to correct for variability in the speed of participant responses, both the stimuli and participant responses are interpolated such that there are an equal number of points in each trajectory spaced evenly along their length. The

length of the interpolated vector is set as the length of the longer of the two input trajectories, the response or the stimulus. Subsequently, the change in turn angle is calculated as the change in the trajectories interior angle (relative to the closed trajectory) between consecutive points. The difference in turn angles is then minimized between the stimulus and response using DTW and the “mori2006” step pattern which constrains the number of times DTW can reuse elements of the stimulus or response trajectories (Giorgino, 2009). This step creates comparisons between the stimulus and response trajectories that is based on the features (corners, loops, convex or concave curves) present in each trajectory. Subsequently the Procrustes analysis is used to align the response to the stimulus trajectory of the newly generated comparison mapping from DTW. The result of this analysis is error as well as the correlation between the change in turn angles between points in the stimulus and response trajectories. We believe that this correlation measure is a better representation of the intended movement as correlations are not affected by the physical space between or orientation of the response to stimulus trajectories; instead, this correlation-based measure represents the degree of similarity between features in each trajectory.

#### *3.3.4 Statistical Analysis:*

Each outcome measure was assessed using the same hierarchal Bayesian linear mixed effect models using stan and brms (version 2.19.0; Bürkner, 2017). All variables were scaled to unit variance (mean=0, SD=1) and log transformations were used when appropriate. Weakly informed regularizing priors were used for all models under the assumption that the mean for each coefficient would fall within 2 standard deviations of the data. The models tested the differences in performance (error (px)) between the employed analyses (original and updated),

assessing any interactions between the analysis and other independent variables in the model including figure type (random and repeated), group (PP, PPFB, MI and PC), trajectory complexity (the sum of the interior turn angles), and the stimulus animation velocity (px/s; Equation 3.1). Note that the model supports interactions between all terms except the interaction of complexity and figure type, as the repeated trajectories only had one level of complexity for each participant. This model also included a random intercept term for each participant and random slopes for the analysis used: stimulus animation velocity and figure type. A half sum contrast was used for all variables, including group whereby each experimental group was contrasted against the perceptual control group.

A second model was used to determine if the effects of motor imagery training could be realized using a turn angle correlation-based outcome measure predicted using block (1:5), figure type (random and repeated), group (PP, PPFB, MI and PC), trajectory complexity (the sum of the turn angles) and stimulus animation velocity (px/s; Equation 3.2). In this model the MI group's performance on the 5<sup>th</sup> session was compared to the 5<sup>th</sup> session of the PC group and the 1<sup>st</sup> session of the PPFB and PP groups as these timepoints represent the first exposure for each of the four groups to overt execution of the task. This model also included a random intercept term for each participant and random slopes for stimulus animation velocity and figure type. A half sum contrast was again used for all variables, including group where each experimental group was contrasted against the MI group. The posterior distribution was then sampled and transformed back to their original scale to visualize the credible effects, which were assessed according to the Bayesian Analysis Reporting Guidelines (Kruschke, 2021). For the first model, visualizations of credible effects were constrained to those involving the term for analysis used



to determine the effect of the analysis and in the second model all credible effects were visualized.

$$Error_i = N(u_i, \sigma)$$

$$u_i = B_{Analysis[i]} * B_{Condition[i]} * B_{Figure\ Type[i]} * B_{Animation\ Velocity[i]} + B_{Complexity[i]} \\ + B_{Complexity:Analysis[i]} + B_{Complexity:Condition[i]} \\ + B_{Complexity:Animation\ Velocity[i]} + B_{Complexity:Analysis:Condition[i]} \\ + B_{Complexity:Analysis:Animation\ Velocity[i]} \\ + B_{Complexity:Condition:Animation\ Velocity[i]} \\ + B_{Analysis:Condition:Complexity:Animation\ Velocity[i]} + (1 + B_{Analysis[i]} \\ * B_{Figure\ Type[i]} * B_{Animation\ Velocity[i]} | B_{Participant[i]}/)$$

$$B_{effect} \sim N(0, 2)$$

$$B_{participant} \sim N(0, \sigma_{participant})$$

$$\sigma_{participant} \sim Exponential(1)$$

$$\sigma \sim Exponential(1)$$

Equation 3.1: The full model specification used to compare the two analyses' ability to predict error from the complex movement execution paradigm.

$$Correlation_i = N(u_i, \sigma)$$

$$\begin{aligned}
u_i = & B_{Block[i]} * B_{Condition[i]} * B_{Figure\ Type[i]} * B_{Animation\ Velocity[i]} + B_{Complexity[i]} \\
& + B_{Complexity:Block[i]} + B_{Complexity:Condition[i]} + B_{Complexity:Animation\ Velocity[i]} \\
& + B_{Complexity:Block:Condition[i]} + B_{Complexity:Block:Animation\ Velocity[i]} \\
& + B_{Complexity:Condition:Animation\ Velocity[i]} \\
& + B_{Complexity:Block:Condition:Animation\ Velocity[i]} + (1 + B_{Figure\ Type[i]} \\
& * B_{Animation\ Velocity[i]} | B_{Participant[i]}) \\
& B_{effect} \sim N(0,2) \\
& B_{participant} \sim N(0, \sigma_{participant}) \\
& \sigma_{participant} \sim Exponential(1) \\
& \sigma \sim Exponential(1)
\end{aligned}$$

Equation 3.2: The full model specification used to determine the effect of motor imagery training on subsequent overt execution using a correlation-based outcome measure.

### 3.4 Results:

#### 3.4.1 Participants and descriptive results:

After removing participants who didn't complete the protocol or had too many erroneous trials, fifty-six participants were left in the final analysis spread across the four groups (Table 3.1). The larger number of participants dropped relative to Ingram et al., (2019) reflects the stricter criteria of the step pattern used in DTW, which caused an additional 5 participants to be removed from the analysis. The analyses produced differing values of error, whereby the magnitude of error was higher on trials processed using the updated analysis, however the differences between figure type for each group remained similar across analyses (Figure 3.1). The most notable improvement of the analysis is best described by a visual inspection of

example trials where features of the stimulus are much better aligned with the corresponding features in the participants' responses (Figure 3.2). Figures 3.2A-C demonstrate limitations of the original analysis process that are overcome with the updated analytic approach whereby: 1) there was a tendency to endlessly reuse points due to the unconstrained step pattern (Figure 3.2A), 2) points were paired based on spatial proximity rather than the features of the trajectory (Figure 3.2B) and 3) a severe lack of samples in trajectories that were animated at higher speeds (Figure 3.2C).

Table 3.1: Demographic information of the 4 experimental groups.

GROUP	SAMPLE SIZE	AGE (mean±SD)	SEX (F:M)	HANDEDNESS (L:R)
PC	15	22.1±2.8	F = 12 : M = 3	L = 1 : R = 14
MI	16	24.2±5.7	F = 11 : M = 5	L = 1 : R = 15
PPFB	13	23.7±4.2	F = 7 : M = 6	L = 0 : R = 13
PP	12	23.4±4.0	F = 8 : M = 4	L = 1 : R = 11

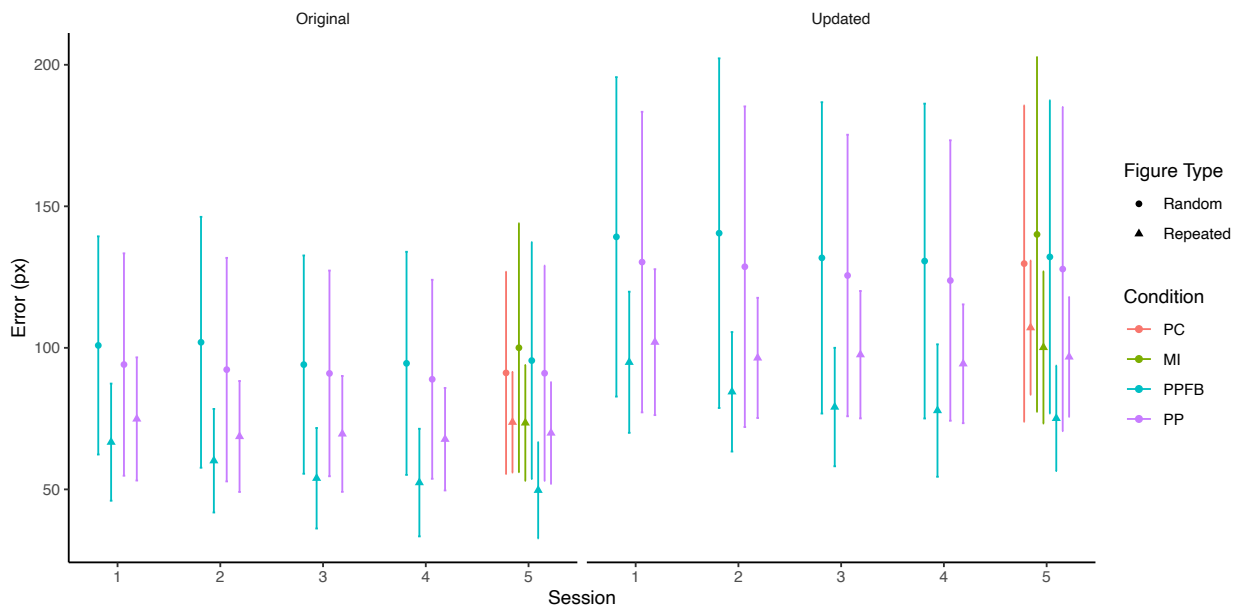


Figure 3.1: A visualization of the descriptive results separated by session and the categorical variables in the analysis. The subplot on the left represents the original analysis from Ingram et al., (2019) and the subplot on the right represents the updated analysis. Error is reported across each session and organized into each group in the study (PC: red, MI: green, PPFB: blue, PP: purple).

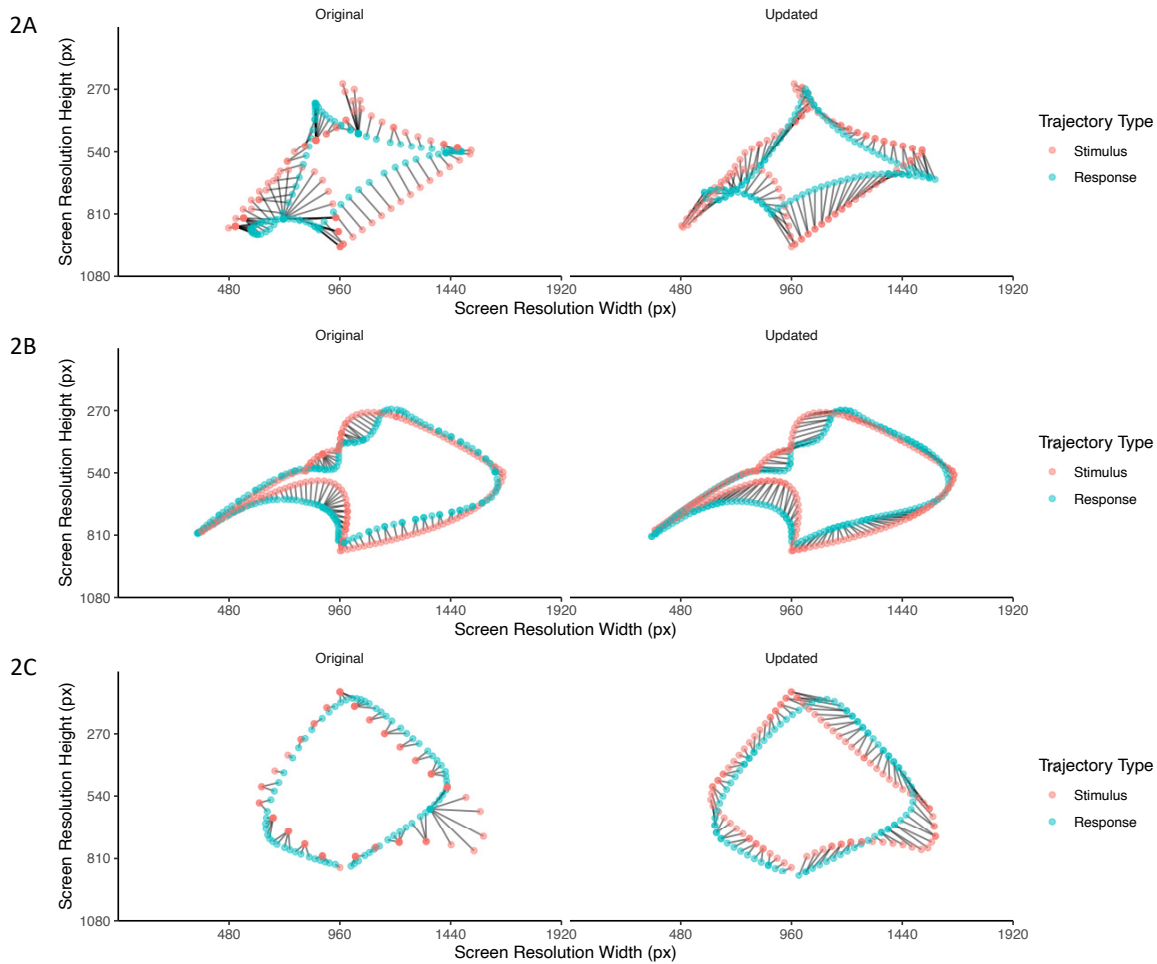


Figure 3.2: Visualizations of the error calculations for a trial resulting from each analysis. Figures 2A and B visualize trials with one of the repeated stimulus trajectories and 2C visualizes performance on a random stimulus trajectory from 3 different participants. In each figure, the results of the original analysis from Ingram et al., (2019) is pictured on the left and the updated analysis is on the right. The participant response is denoted by the red series of dots and the stimulus trajectory is represented by the blue series. Error on a given trial is represented by the length of the black lines whereby the average line length is the error metric used in subsequent statistical modeling.

### 3.4.2 Effects of the updated analysis:

The comparison of the two analyses revealed a credible effect of the analysis used (beta coefficient ( $\beta$ ): -0.31 [89% highest posterior density interval (HPDI): -0.34:-0.27], maximum probability of effect (MPE): 1, percent overlap with the region of practical equivalence (ROPE): 0) and credible interaction between the analysis used and the stimulus animation velocity ( $\beta$ : 0.18 [0.15:0.22], MPE: 1, ROPE: 0). An additional three-way interaction denoted a probable

effect of the analysis used and figure type on the comparison of the PPFB to PC group, but the effect was partly contained within the region of practical equivalence ( $\beta$ : -0.22 [-0.47:0.01], MPE: 0.93, ROPE: 0.18). For interpretation only the highest order effects were visualized. The main effect of the analysis demonstrates that the updated analysis resulted in a higher mean error on trials in comparison to the original analysis from Ingram et al., (2019), which was realized largely by increased error in trials where the stimulus was presented slowly to participants (Figure 3.3). The three-way interaction between the PPFB and PC group in the updated analysis, and figure type demonstrated that the learning effect (i.e., the difference between figure types), in the PPFB group is more pronounced in comparison to the PC group when using the updated analysis (Figure 3.4).

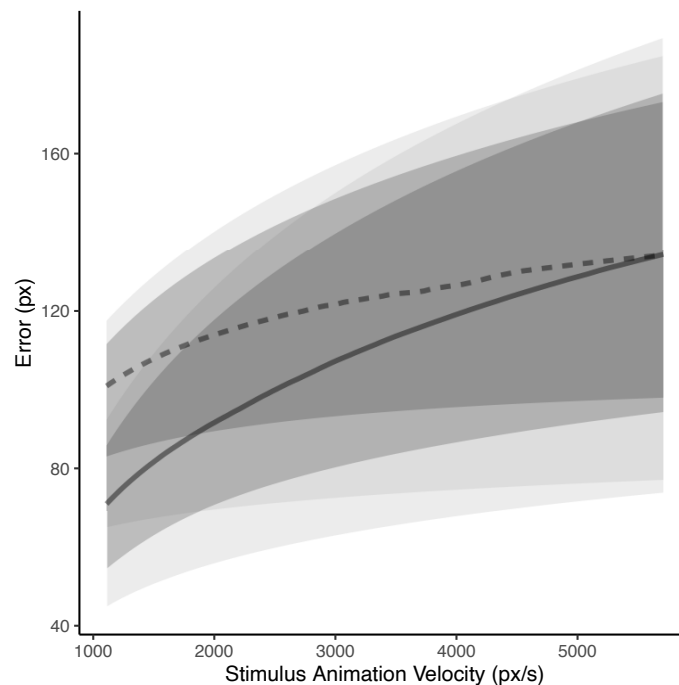


Figure 3.3: A visualization of the credible interaction between stimulus animation velocity and analysis used on error. The dashed line represents median error from the updated analysis and the solid line represents the median error attained from the original analysis. The ribbon represents the 60<sup>th</sup> and 90<sup>th</sup> quantiles.

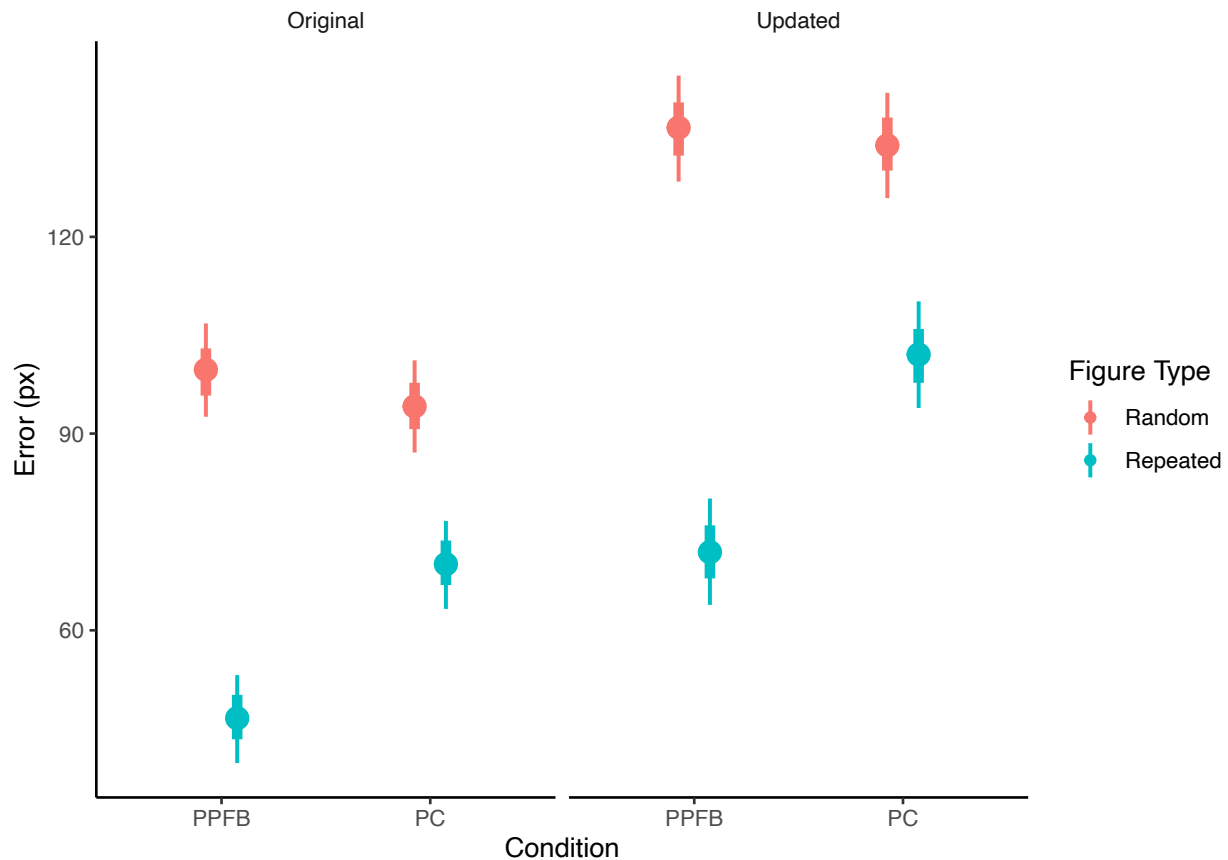


Figure 3.4: Visualizations of the interaction between figure type, analysis used, and the PPFB and PC groups on error. Error is reported as the median  $\pm$  [60 and 90%HPDIs]. The subplot on the left represents the original analysis from Ingram et al., (2019) and the subplot on the right represents the updated analysis. Error is reported across each group (PC and PPFB) and organized by figure type (Random: red, Repeated: blue).

### 3.4.3 Correlation-based analysis:

Using the correlation between consecutive turn angles as the dependent variable instead of error there are discernable differences between the MI group and both the PC and PPFB groups. Specifically, there was a credible main effect of figure type ( $\beta$ : -0.44 [-0.58:-0.29], MPE: 1, ROPE: 0) and a probable interaction of figure type and the contrast between the PC and MI groups ( $\beta$ : 0.47 [-0.01:0.96], MPE: 0.94, ROPE: 0.09) that were captured in a credible three-way interaction of the contrast between the MI and PC groups, stimulus animation velocity and figure type ( $\beta$ : 0.57, [0.18:0.96], MPE: 0.99, ROPE: 0) (Figure 3.5). This effect

denotes that in the MI group participants had higher correlations on the repeated trajectories that were more resistant to increases in stimulus animation velocity (Figure 3.5). Additionally, there was a probable interaction between the contrast of the MI and PPFB groups with stimulus animation velocity and figure type that was slightly contained in the ROPE ( $\beta$ : -0.28 [-0.65:0.10], MPE: 0.88, ROPE: 0.18) (Figure 3.5). This interaction demonstrates that the correlation between the random trajectories and the corresponding stimulus was similar in both groups across the range of stimulus animation velocities, but the repeated trajectory correlations were higher in the PPFB group and seem to increase slightly as stimulus animation velocity increased in contrast to the MI group where correlations decreased with faster stimulus animation velocities (Figure 3.5). Lastly, there was also a probable main effect of complexity, whereby correlations decreased as a function of increasing complexity ( $\beta$ : -0.15 [-0.21:-0.09], MPE: 1, ROPE: 0.06) (Figure 3.6).

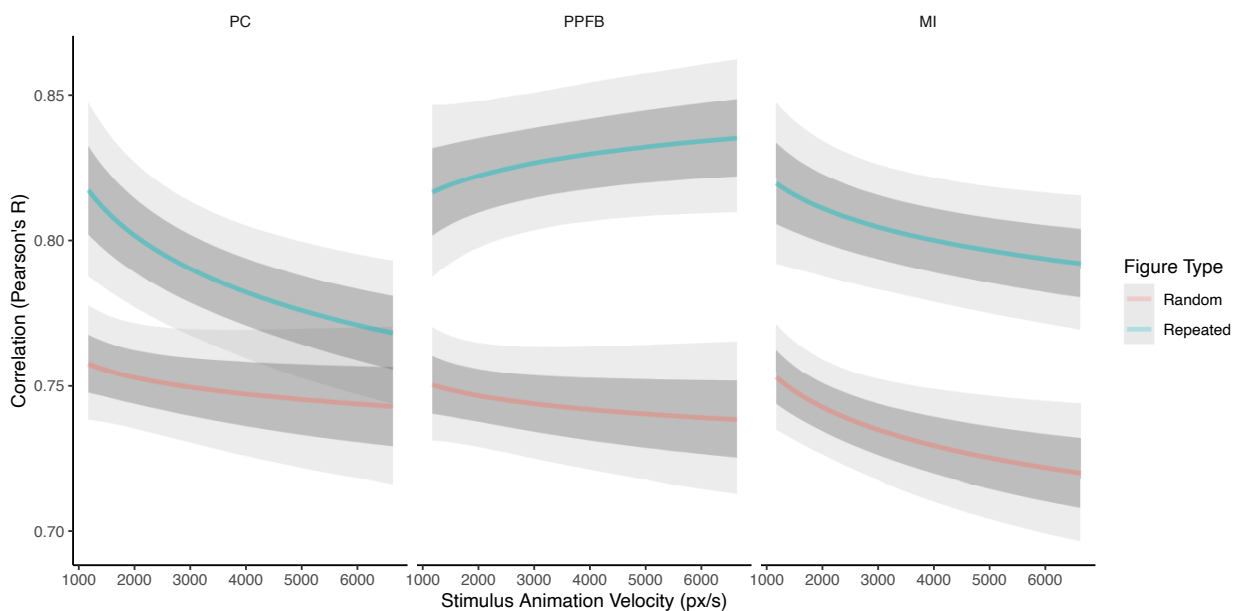


Figure 3.5: Visualizations of the interactions between group, stimulus animation velocity and figure type. Red series denote the median correlation between stimulus and response on random figures and the blue lines represent the



median correlation for the repeated trajectories across the range of stimulus animation velocities. The visualization is divided into facets based on group. The ribbon represents the 60<sup>th</sup> and 90<sup>th</sup> quantiles.

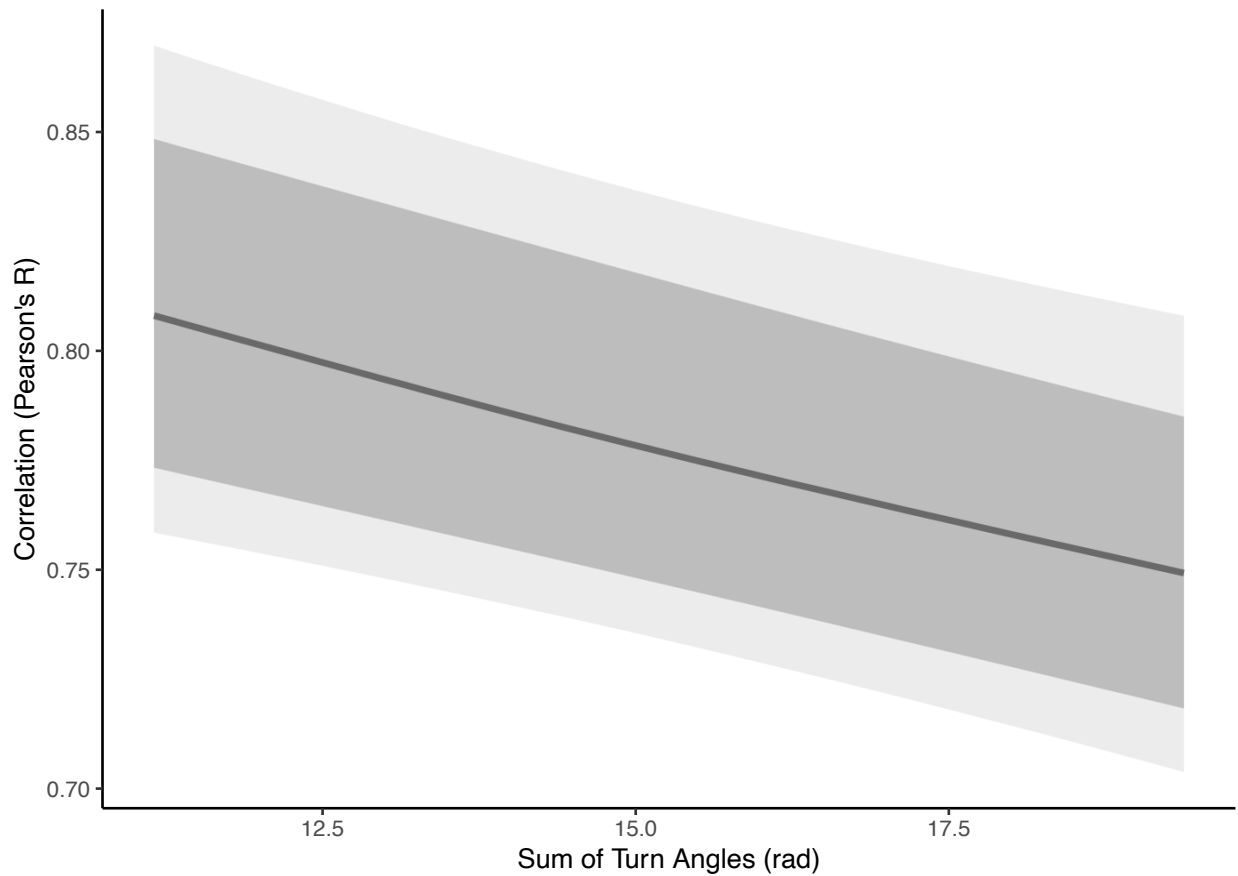


Figure 3.6: A visualization of the effect of complexity (sum of turn angles) on the correlation between stimulus and response. The line represents the median correlation values a ribbon representing the 60<sup>th</sup> and 90<sup>th</sup> quantiles.

### 3.5 Discussion:

The updated analyses employed in this study provide a novel method for evaluating data produced by the complex movement execution paradigm which results in a promising alternative to the standard error-based metrics for evaluating performance on a continuous motor task. The updated analysis resulted in higher error on slowly animated trajectories and suggests a larger benefit of the PPFB training in comparison to the original analysis (Figures 3 and 4). While this did not achieve the objective for success as the updated analysis seems to be minimally affecting the differences in the interactions between the other predictors, we believe

that this difference is acceptable in light of the examples provided in Figure 3.2, where the turn angle-based application of DTW both appears qualitatively to be producing more accurate comparisons between stimulus and response trajectories in a variety of instances. With respect to the goal of establishing a new outcome measure for this paradigm, the correlations of turn angles denoted a hierarchical impact of group on the similarity of the repeated trajectory across stimulus animation velocities whereby the PPFB group produces the most similar trajectories across the different stimulus animation velocities followed by the MI and the PP group and, lastly, while the PC group had the worst performance across the different stimulus animation velocities (Figure 3.5). This effect aligns with the published findings of Ingram et al., 2019 that note the most effective performance, as defined by the steepest point of an error based non-linear speed accuracy function, occurred in the PPFB group, followed by the MI and PP group and the worst performance was obtained by the PC group (T. G. J. Ingram et al., 2019).

### *3.5.1 Updated Analysis:*

Firstly, interpretation of the model describing the impact of the analysis used was constrained only to the credible effects and interactions of the analysis term used due to difficulties in comparing a linear mixed effect model against the statistical approach used in Ingram et al., (2019). The differences in the model specification and outcome measures between this study and the original publication limited our ability to meaningfully compare results of the different modelling approaches as they use different terms to account for the predictors of interest in different manners. We believe that the model used in the original study is a more accurate representation of the data, thus the current re-analysis of the data constrained its interpretation to terms that evaluate the benefits of the updated analysis. To

address the purpose of this study, we tested for the presence of interactions between the analysis term and other categorical predictors would violate the a-priori objective of consistent inter group differences between the two analysis pipelines. The updated analysis did not meet this objective as there was the interaction between figure type and the comparison of the PPFB to PC groups. Specifically, the updated analysis suggests an increased benefit of the PPFB group's training on learning (i.e., the difference between performance on random and repeated trajectories within group), relative to the PC group. This deviation from the objective of consistent inter group differences between analyses seems acceptable since the updated analysis appears to be more sensitive to the learning in the PPFB group which was already the most effective condition for learning (T. G. J. Ingram et al., 2019). Additionally, we believe this analysis is a vast improvement over the original analysis as it better addresses several limitations of the previous paradigm (Figure 3.2A-C). Due to the natural distribution of samples in response trajectories where more samples are recorded in corners rather relative to straighter lines, the unconstrained step-pattern used in DTW identified "anchor" samples in the response trajectories that get re-used for many comparisons in the subsequent Procrustes analysis. The unintended effect of this decision was that the Procrustes transformations would be heavily biased towards these anchor points and ignore other features the response trajectory. The combination of using interpolation to evenly spread the distance between samples and the use of the mori2006 step pattern in DTW eliminates this issue as confirmed via visual inspection of Figure 3.2A whereby each sample in the stimulus trajectory is only reused once or twice at most to compare to the response trajectory. As a result, the Procrustes analysis better centers the response trajectory to the stimulus in comparison to the original analysis

where the response trajectory gets tilted towards two heavily sampled points in the lower left-hand corner of the trajectory and two points in the uppermost section (Figure 3.2A). Using DTW to pair samples from the stimulus to response trajectories appears to create more logical comparisons and also explain the increased error obtained when using the updated analysis. Using Figure 3.2B as an example of this effect, the original analysis minimizes error between the two trajectories causing pairings of the two crests of the curves in the uppermost portion of the stimulus trajectory to the valleys of the curve in the corresponding response trajectories. When using DTW to minimize the turn angle between consecutive samples in each trajectory the new analysis aligns samples at the crest of the curves in the repeated trajectory to those in the response trajectory. Although this pairing introduces a greater amount of error on the trial, we believe that the corresponding pairing of samples from each trajectory is more logical. Lastly, the updated analysis is able to better capture error on quickly animated trials as the interpolation step allowed the stimulus to be up sampled to the length of the response trajectory. The original analysis had much fewer samples in the stimulus trajectories contributing to the aforementioned anchoring issue. Figure 3.2C visualizes the benefit of interpolation whereby the stimulus trajectory can be up sampled to facilitate a better pairing with the response trajectory on the trial.

### 3.5.2 *Correlation outcome measure:*

The purpose of the novel turn angle correlation outcome measure was to quantify improvements made in action selection by evaluating the control policy that governs movement separately from the execution of the produced motor commands (Krakauer et al., 2019; McDougle et al., 2015; Taylor & Ivry, 2011; Todorov & Jordan, 2002). Since learning in motor

imagery is thought to be reflective of this process, in part due to the lack of overt execution, it would be advantageous to select an outcome measure that measures the accuracy of a control policy regardless of how accurately it was performed (Dahm & Rieger, 2019b; Frank & Schack, 2017; S. N. Kraeutner, Keeler, et al., 2016). The complex movement execution task provides a unique situation to create a measure that addresses the above statement by comparing the degree of similarity between the stimulus and response trajectory via correlations. We believe that a correlation is a good measure of what the control policy is for a movement as it is independent of the spatial differences between the stimulus and response trajectories and, as such, is a better representation of the selected movement than an error-based metric. In this study the correlation metric revealed three meaningful effects: 1) complexity of the stimulus shape negatively impacted the correlation of turn angles between stimulus and response, 2) correlations between the responses and the repeated trajectory were retained across stimulus animation velocities in the MI group relative to the PC group, and in turn, 3) correlations between the responses and the repeated trajectory were retained across stimulus animation velocities in the PPFB group relative to the PC group. These effects align with the finding of Ingram et al., (2019) which demonstrate benefits of motor imagery training over a perceptual control group and overt execution training. Further, the above-noted effects indicate this updated analysis achieved the present study's second objective, which was to establish an outcome measure that is a better representation of the control policy generated during action selection. Surprisingly, the slope of the relationship between correlation and stimulus animation velocity for the repeated trajectory in the PPFB group has a slight positive slope indicating that the correlations increased minimally as a function of time. This result is unintuitive but given

that a horizontal line drawn through the intercept is barely contained in the 60% quartile at all levels of stimulus animation velocity, the direction of this slope is likely not worth interpreting, and rather, the conclusion drawn from this result is that stimulus animation velocity didn't strongly impact the correlations in this group. The resulting interaction between the comparison of the PPFB and MI group, stimulus animation velocity, and figure type demonstrated that over 100 trials of overt execution with the provision of feedback, participant's performance on the repeated trajectory eclipsed the performance of participants that performed 400 previous imagery trials. This conclusion again aligns with Ingram et al., (2019) whereby the magnitude of learning is significantly increased by performing the task overtly and the provision of feedback.

### 3.6 Conclusion:

The updated analysis employed in this study did not meet the *a-priori* objective for analysis as it mediated effects of other factors used to predict performance on the task in a manner dissimilar to the original analysis. However, the deviation was not impactful on the conclusions drawn from the results and the qualitative improvements to the resulting error calculations validate its use in future studies. Additionally, the novel outcome measure met its objective by demonstrating a meaningful improvement of imagery training on the complex movement execution task relative to the perceptual control group and serves as a promising approach to evaluating the accuracy of the control policy used to govern movement in future applications of this paradigm.

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## Chapter 4: Cortical regions involved in motor imagery-based motor learning

### 4.1 *Abstract:*

Motor imagery performance is underpinned by a network of cortical regions including the inferior parietal lobe and premotor regions. Past research has investigated the role of these regions by impairing their function using repetitive transcranial magnetic stimulation (TMS) and observing the effect on motor imagery-based motor learning. These studies found that stimulation delivered to the left inferior parietal lobe (L\_IPL) and supplementary motor area (SMA) impairs motor imagery-based motor learning but stimulation to the M1 did not. A caveat to this result is that the employed task, a version of the serial reaction time task, is biased towards improvements in goal and action selection rather than action execution due to the kinematic simplicity of the required movement. As such, past findings could be reflective of the cognitive nature of the task used rather than the nature of MI, thus confounding the results and their subsequent interpretation. Here we use the same design as the original studies whereby repetitive TMS was applied to each of the same cortical regions (L\_IPL, M1, SMA), but rather than using a task biased to goal and action selection, participants performed a task emphasizing action execution. Results from the L\_IPL aligned with past literature, demonstrating a negative effect of L\_IPL inhibition on motor learning, whereas stimulation to the SMA and M1 facilitated motor imagery-based motor learning. This inability to reproduce previous results speaks to the importance of using a battery of tasks when making inference about the modalities used to learn motor skills, as only results from the L\_IPL are likely to reflect a function that is critical to motor imagery performance.

## 4.2 *Introduction:*

Motor imagery is capable of driving performance improvement or motor skill acquisition (Bonassi et al., 2020; T. G. J. Ingram et al., 2019; Solomon et al., 2022). While motor imagery has been thought to be a parallel process to overt execution, recent studies have demonstrated that imagery relies more on perceptual components of movement to drive motor learning than overt execution (T. G. Ingram et al., 2016; Jeannerod, 2001; T. Kim et al., 2017). This has led to a number of theories that seek to explain the mechanisms behind motor imagery, with these theories broadly placed into two positions based on their belief that the motor system is engaged in motor imagery or if it is more perceptual in nature (see section 1.5 What is motor imagery; Glover & Baran, 2017; Grush, 2004; Jeannerod, 2001; T. Kim et al., 2017). These perceptual components of motor control are often referred to as the planning stage where important variables such as goal and action selection are specified to generate a control policy, a ruleset that governs subsequent action execution, that minimizes the movement cost and maximizes the chance of a successful movement outcome (Gallivan et al., 2018; Krakauer et al., 2019). Behavioural studies have investigated how motor imagery can drive changes in the control of movement and demonstrated that motor imagery training leads to better structuring of movement dendrograms than overt execution, highlighting motor imagery's bias towards improving the accuracy of action selection (T. Kim et al., 2017). These behavioural biases are accompanied by differences in the underlying functional anatomy that highlights motor imagery's reliance on premotor and parietal regions of the cortex involved in state estimation, sensorimotor integration, action selection and movement sequencing (Haar & Donchin, 2020; Hardwick et al., 2018; Lara et al., 2018).

However, activation of a cortical region is ineffective in assessing its role as the region could be involved in a variety of different functions for a given behaviour or represent an abstracted role in a broader set of unmeasured behaviours (Poldrack, 2010). Therefore, the importance of several regions in motor execution and imagery networks, including the left inferior parietal lobe (IPL), motor cortex (M1) and supplementary motor areas (SMA), were assessed in previous literature by observing the effectiveness of skill acquisition when the excitability (and in turn function) of a given brain region was transiently reduced by repetitive transcranial magnetic stimulation (TMS; Huang et al., 2005; S. N. Kraeutner, Keeler, et al., 2016; S. N. Kraeutner, Ingram, et al., 2017; Solomon et al., 2021). In these paradigms, repetitive TMS was delivered to one of the highlighted cortical regions prior to engaging in a serial reaction time task (SRTT) to inhibit the target region before the participants trained on the task. The stimulation group was then compared to a control condition that either did not receive stimulation or received sham stimulation to determine if behaviour was affected. The results obtained using this method suggest that the L\_IPL was integral to motor imagery-based learning but M1 was not (S. N. Kraeutner, Keeler, et al., 2016; S. N. Kraeutner, Ingram, et al., 2017). The role of the SMA was ambiguous as transient impairment of SMA function negatively impacted the acquisition of stimulus response mappings in the task but had no effect on improvements in action execution (Solomon et al., 2021). The summation of this body of work supports the existing neuroimaging evidence that motor imagery relies on perceptual processes to drive motor learning, though the exact roles of these areas in motor imagery remain unclear (Poldrack, 2006). The role of these cortical region was not discernible from the previous literature as the form of repetitive TMS used in the original studies inhibited the target cortical

regions for 45-60min rendering it impossible to ascribe a precise mechanism to areas seemingly involved in motor imagery-based motor learning, the L\_IPL and SMA (Huang et al., 2005). To elucidate the roles of these areas, a much more temporally precise form of stimulation would need to be applied to momentarily interfere with an areas function while performing a task as each area is likely to be involved in several functions over the course of repeated movement. Given the importance of the L\_IPL to motor imagery-based motor learning, a recent study inhibited this area immediately after each trial during motor imagery training with little effect on motor learning (see Chapter 2; Solomon et al., 2022).

Stemming from the null result from Solomon et al., (2022) is the unknown effect of task complexity on the neuroanatomical demands of imagery (Hardwick et al., 2018). Many studies of motor learning that employ neuroimaging methodologies use simple tasks, such as SRTTs, as they are well established and are amenable to perform alongside neuroimaging as the movements are smaller in magnitude and less likely to cause head movements which can create artifacts in the neuroimaging data (Puce & Hämäläinen, 2017). In these tasks, participants are exposed to and respond to a seemingly random sequence of cues with a button press. A subset of these cues repeats throughout the experimental session interlaced with randomly generated cues (Robertson, 2007; Schwarb & Schumacher, 2012). After training, participants learn to respond faster to the repeated cues in comparison to the randomly generated ones by strengthening the relationship between a stimulus and the subsequent (well-practiced) response, a button press (S. N. Kraeutner, Gaughan, et al., 2017; Robertson, 2007; Schwarb & Schumacher, 2012; Wilkinson & Shanks, 2004). The SRTT and variations on the SRTT rely on improvements to goal and action selection in contrast to more typical, complex motor tasks

seen in vocational, athletic, musical or rehabilitation settings that rely on improvements to action execution (Krakauer et al., 2019). Rather than relying on stimulus response associations, tasks that rely on improvements to action execution use the process of monitoring movement throughout its performance and knowledge of the movement's result to guide learning (Haar & Donchin, 2020; McNamee & Wolpert, 2019; Shadmehr & Krakauer, 2008; Wolpert & Flanagan, 2016). Given that the importance of the L\_IPL to motor imagery-based learning was elucidated in an experiment using an SRTT, it is conceivable that the tasks used to investigate the nature of motor imagery is creating a bias in the literature where the perceptual nature of motor imagery is over-emphasized. These tasks often rely on stimulus response mappings as opposed to ones that require improvements in action execution emphasizing the importance of functional brain activity in areas supporting goal and action selection (S. N. Kraeutner, Gaughan, et al., 2017; Schwarb & Schumacher, 2012).

To test if a task related bias is impacting the generalizability of the conclusion that motor imagery is more perceptual in nature, this study aimed to determine if the results of repetitive TMS applied to the L\_IPL, M1 and SMA would be the same for a complex motor task (see the complex movement trajectory described in Chapter 2 and 3), which relies on improvements in action execution, as the results found for the modified SRTT used in the original experiments (S. N. Kraeutner, Keeler, et al., 2016; S. N. Kraeutner, Ingram, et al., 2017; Solomon et al., 2021). One hundred and fifty-six participants were recruited to engage in a complex movement execution task over two sessions. Prior to performing the task in the first session participants received either sham stimulation over the vertex of their head or continuous theta burst stimulation to their L\_IPL, M1 or SMA. They would subsequently perform 80 training trials using

motor imagery or overt execution before finishing the session with a 20-trial overt execution test block. In the second session participants repeat the test block from session 1 to assess retention. Performance on the task was compared between stimulation and sham conditions to see if the stimulation affected performance. Based on the original series of studies that used an SRT-like task, separate hypotheses were made for each cortical region of interest. Specifically, it was hypothesized that in motor imagery, stimulation to the L\_IPL will reduce the degree of learning on the task, whereas in the overt execution condition stimulation to the M1 will impair performance, aligning with the finding of Kraeutner et al., (2016) and (2017).

#### **4.3 Methodology:**

##### **4.3.1 Participants:**

One hundred and fifty-six 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. 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). Participants were randomly assigned to one of six groups based on a combination of modality (overt execution or motor imagery) and stimulation target (L\_IPL, M1 or SMA). If resting motor threshold (RMT) could not be found for a participant (see section 4.3.4. transcranial magnetic stimulation for details) they were then rolled into a sham condition, creating 8 total groups in the study (ME\_SHAM, MI\_SHAM, ME\_IPL, MI\_IPL, ME\_SMA, MI\_SMA, ME\_M1, MI\_M1). Resting motor threshold is not always found for each participant due to a variety of factors including but not exclusive to inter-participant differences in their sensitivity to TMS, skull thickness, poor co-registration with

the template MRI and hairstyles that prevent the coil from resting on the scalp. 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.

#### 4.3.2 *Task Description:*

The task used in this study requires participants to re-create animated trajectories on a touch screen with their index finger using either motor imagery or execution depending on the group designation (T. G. J. Ingram et al., 2019); this task was also used in Chapter 2 and 3; <https://github.com/LBRF/TraceLab>). Participants used a 24" touch screen monitor with 1080p resolution and 60Hz refresh rate (Planar Helium PCT2485) located approximately 12" in front of them, lying flat on a table, to complete the task. This orientation of the touchscreen allowed for unobstructed viewing and for the participant to comfortably reach the screen. Each trial consisted of two phases: a stimulus presentation, and a participant response. During the stimulus presentation a white dot would trace out a trajectory built of 5 connected Bezier curves, which started and ended on an indicated point on the midline of the screen. Stimuli were grouped into one of two classes, random and repeated. Random trajectories were generated at the beginning of each trial, whereas the repeated trajectory, a single trajectory, was decided at the onset of the experiment and interspersed evenly throughout each block of the experiment at a 1:1 ratio with random trajectories. Each trajectory was animated in a clockwise direction at one of five durations, 500, 1000, 1500, 2000, and 2500 milliseconds (ms), such that participants were exposed evenly to each combination of animation duration and trajectory class. Participant responses were made using motor imagery or execution as appropriate for the block (see experimental overview). Participant responses began by a red



circle appearing on the touchscreen appearing on the start / end point of the trajectory.

Participants responding via imagery would then place their index finger on the red circle, at which point it turned green, prompting the participant to imagine themselves performing the movement at the speed that it was animated (i.e., completing the trajectory at one of the five animation durations). Once participants imagined their hand returning to the start / end point of the trajectory they would lift their hand off the screen ending the trial. Responses via overt execution occurred in a similar manner to motor imagery except that participants would physically trace the trajectory on the touch screen matching the animation duration.

#### *4.3.3 Experimental Overview:*

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. Transcranial magnetic stimulation was then used to obtain the participant's resting motor threshold (RMT) and continuous theta burst stimulation was subsequently delivered to inhibit the region of the brain corresponding to the group designation (see Transcranial Magnetic Stimulation below). If RMT could not be found on the participant, they were rolled into a sham group and stimulation was given to participants over the vertex of their head. A 10-minute break was then taken before participants engaged in the behavioral task. 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. This block organization resulted in 50 trials of both the

random and the repeated trajectory distributed evenly across animation durations. The first four blocks of the experiment were completed using motor imagery or execution as per the participant's group designation and the final block, the test block, was completed using overt execution. Approximately 24 hour later, participants returned to the laboratory to complete a retention test, which was a replication of the test block at the end of session 1. A detailed timeline is shown in Figure 4.1.

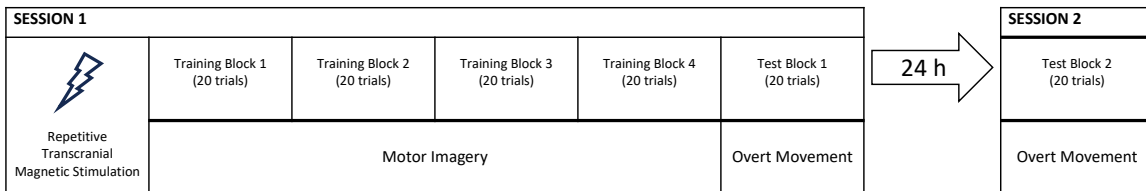


Figure 4.1: Experimental timeline. Following informed consent, screening and questionnaires, participants were given rTMS to either their L\_IPL, M1 or SMA depending on group designation or SHAM stimulation, and then completed 4 blocks of training via motor imagery, followed by a test block of 20 trials 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.

#### 4.3.4 Transcranial Magnetic Stimulation:

Neuro-navigated TMS was performed using an air-cooled 70-mm figure of eight coil connected to a SuperRapid<sup>2</sup>Plus<sup>1</sup> system (Magstim, Whitland, UK) coupled with a Brainsight<sup>TM</sup> system (Rogue Research Inc., Montreal, Canada). For neuro-navigation, each participant's head was co-registered to a template magnetic resonance image (MNI152\_T1\_1mm) by digitizing three anatomical landmarks (left and right pre-auricular points and the nasion). Resting motor threshold was determined by measuring the peak-to-peak amplitude of the motor evoked potential induced by the application of TMS. Motor evoked potentials were obtained using a baseline corrected signal from EMG electrodes overlying the first dorsal interosseous muscle

using vendor supplied hardware (Brainsight2™ EMG Isolation Unit and Amplifier Pod).

Identification of RMT was facilitated by superimposing a 5x5 grid with 7.5 mm spacing on the template magnetic resonance image with the center of the grid overlying the 'hand knob' of the primary M1. Points on the grid were stimulated to identify the location where the lowest stimulator intensity produced motor evoked potentials of  $>50 \mu\text{V}$  on 5 of 10 stimuli. This location was determined to be the 'hotspot' (Kleim et al., 2007). Throughout, the TMS coil was positioned tangentially to the participant's scalp at a  $45^\circ$  angle to the anterior-posterior axis. After RMT was determined, participants received inhibitory stimulation to either the L\_IPL (-36, -23, 34 [X, Y, Z]; MNI space; S. N. Kraeutner, Keeler, et al., 2016), M1 (at the hotspot identified for that participant's first dorsal interosseous) or SMA ( $x = -6, y = -16, z = 75$ ; Solomon et al., 2021). If participants were unresponsive to the stimulation, they were given sham stimulation in lieu of inhibitory stimulation. Inhibitory stimulation delivered to the SMA followed an established continuous theta burst stimulation protocol (Huang et al., 2005; Oberman et al., 2011) consisting of bursts of three stimuli at 50Hz pulses, repeated at intervals of 200ms for a total of 600 pulses delivered at 90% of the participants RMT (Nyffeler et al., 2008). Sham stimulation consisted of the same continuous theta burst stimulation protocol with stimulation intensity set to 20% of stimulator output and the TMS coil placed over the vertex of the head.

#### 4.3.5 Data Analysis:

Analysis procedures were based on those reported in Chapter 3 (see section 3.3.3 Data Analysis). Briefly, trials were screened for a variety of touch screen related artifacts. The variability in participant's response speed with reference to the presented stimuli in the remaining trials were handled by interpolating points across each trajectory such that they were

equidistant to each other and equally dispersed across the length of the trajectories. The turn angle between consecutive samples in each trajectory were then calculated and used to guide dynamic time warping to pair appropriate samples from the response and stimulus trajectories (Giorgino, 2009). The resulting pairings were used in a Procrustes analysis that optimally translate, rotate, and scale the response trajectory to best align it with the stimulus (Goodall, 1991). Two outcome measures were used for this study, the first was error (operationalized as the mean Euclidean distance (pixels)) between the stimulus and response trajectories and the second was the correlation of turn angles between stimulus and response trajectories, reported on in Chapter 3. 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 trial's animation duration.

#### *4.3.6 Statistical Analysis:*

Two hierarchical Bayesian linear mixed-effects regressions were used to make statistical inferences regarding group performance on the task across study sessions, one for each outcome variable. All models were run using the “brms” package for R (version 4.3.0).

Each outcome measure was assessed using the same predictor variables (see Equations 4.1 and 4.2 below). Each model used fixed effects of stimulation site (L\_IPL, SMA, M1 and SHAM), practice modality (overt execution and motor imagery), figure type (random and repeated), session (1 and 2), stimulus animation velocity (see Data Analysis) and complexity (sum of the trajectories interior turn angles) to predict each outcome measure. All fixed effects were allowed to interact less complexity as the repeated trajectory only had one level of

complexity (see Equations 4.1 and 4.2). Each participant was assigned a random intercept and random slopes for stimulus animation velocity, session, figure type and their interactions. All variables were scaled to unit variance (mean=0, SD=1) and log or square root transformations were used when appropriate. Weakly informed regularizing priors were used for all models under the assumption that the mean for each coefficient would fall within 2 standard deviations of the data. A half sum contrast was used for all variables, including stimulation site whereby each site was contrasted against the SHAM condition. The posterior distribution was then sampled and transformed back to their original scale to visualize the credible effects, which were assessed according to the Bayesian Analysis Reporting Guidelines (Kruschke, 2021). Due to the number of fixed effect terms in the model (97), only the credible effects were reported and of those effects only the highest order interaction effects are visualized.

$$Error_i = N(u_i, \sigma)$$

$$u_i = B_{Stimulation\ Site[i]} * B_{Practice\ Modality[i]} * B_{Session[i]} * B_{Figure\ Type[i]} * B_{Animation\ Velocity[i]} \\ + B_{Complexity[i]} \\ + (1 + B_{Analysis[i]} * B_{Figure\ Type[i]} * B_{Animation\ Velocity[i]} | B_{Participant[i]})$$

$$B_{effect} \sim N(0, 2)$$

$$B_{participant} \sim N(0, \sigma_{participant})$$

$$\sigma_{participant} \sim Exponential(1)$$

$$\sigma \sim Exponential(1)$$

Equation 4.1: The full model specification used to determine the effect of stimulation site on overt execution and motor imagery training using an error-based outcome measure.

$$Correlation_i = N(u_i, \sigma)$$

$$u_i = B_{Stimulation\ Site[i]} * B_{Practice\ Modality[i]} * B_{Session[i]} * B_{Figure\ Type[i]} * B_{Animation\ Velocity[i]} \\ + B_{Complexity[i]}$$

$$+ (1 + B_{Analysis[i]} * B_{Figure\ Type[i]} * B_{Animation\ Velocity[i]} | B_{Participant[i]})$$

$$B_{effect} \sim N(0, 2)$$

$$B_{participant} \sim N(0, \sigma_{participant})$$

$$\sigma_{participant} \sim Exponential(1)$$

$$\sigma \sim Exponential(1)$$

Equation 4.2: The full model specification used to determine the effect of stimulation site on overt execution and motor imagery training using a correlation-based outcome measure.

#### 4.3.7 Transparency and Openness:

Data were analyzed using *R* version 4.3.0 (R Core Team, 2023) and the packages *tidyverse* version 2.0.0 (Wickham, 2014), *vegan* version 2.6-4 (Oksanen et al., 2023), *TSEntropies* version 0.9, *rStan* version 2.26.22 (Stan Development Team, 2023), *brms* version 2.19.0 (Bürkner, 2017), *tidybayes* version 3.0.4 (Kay, 2023), *parameters* version 0.21.0 (Lüdtke et al., 2020), and *emmeans* version 1.8.5 (Lenth et al., 2023). This study was not pre-registered. All data and analysis code will be publicly available (Github and Open Science Framework) at the time of publication.

## 4.4 Results:

### 4.4.1 Demographics and Descriptive Results:

Of the 156 participants recruited, 32 didn't complete both experimental sessions, 1 participant failed to produce enough usable trials in the second session, 3 participants were removed as

they failed to match the stimulus animation speed during responses and 2 participants were removed based on observation of overt execution during motor imagery training. The final sample included 118 participants (Table 4.1). Mean error and turn angle correlations from both sessions revealed improved performance on the repeated relative to the random trajectories whereby error is lower, and the correlations are higher and contain less variance (Table 4.2, Figures 4.2 and 4.3).

*Table 4.1: Demographic information from the final sample separated by stimulation site and training modality. All means are reported  $\pm$ SD*

<b>Stimulation Site</b>	<b>Practice Modality</b>	<b>Size</b>	<b>Age</b>	<b>Kinesthetic KVIQ</b>	<b>Sex</b>	<b>Handedness</b>
<b>SHAM</b>	Motor Imagery	15	21.1 $\pm$ 2.4	22.3 $\pm$ 2.5	F:11 / M:4	R:14 / L:1 / A:0
<b>SHAM</b>	Overt Execution	15	20.9 $\pm$ 2.4	20.0 $\pm$ 3.8	F:7 / M:8	R:15 / L:0 / A:0
<b>IPL</b>	Motor Imagery	14	23.7 $\pm$ 4.8	22.6 $\pm$ 2.2	F:10 / M:4	R:13 / L:1 / A:0
<b>IPL</b>	Overt Execution	15	23.7 $\pm$ 5.0	20.9 $\pm$ 4.6	F:9 / M:6	R:14 / L:1 / A:1
<b>SMA</b>	Motor Imagery	14	23.5 $\pm$ 4.1	21.6 $\pm$ 3.4	F:9 / M:5	R:13 / L:0 / A:1
<b>SMA</b>	Overt Execution	15	24.1 $\pm$ 5.2	22.2 $\pm$ 3.0	F:9 / M:6	R:15 / L:0 / A:0
<b>M1</b>	Motor Imagery	15	21.3 $\pm$ 2.4	21.1 $\pm$ 4.1	F:8 / M:7	R:14 / L:0 / A:1
<b>M1</b>	Overt Execution	15	23.6 $\pm$ 5.1	20.5 $\pm$ 4.6	F:7 / M:8	R:15 / L:0 / A:0

Table 4.2: Mean error (Px) and correlations (Pearson's R) for random and repeated figure types, separated by stimulation site, practice modality and session. All means are reported  $\pm$ SD

Stimulation Site	Practice Modality	Session	Random Trajectory		Repeated Trajectory	
			Correlation	Error	Correlation	Error
<b>SHAM</b>	Motor	1	0.77 $\pm$ 0.10	135.8 $\pm$ 51.4	0.81 $\pm$ 0.06	115.9 $\pm$ 27.2
	Imagery	2	0.77 $\pm$ 0.10	131.0 $\pm$ 47.1	0.82 $\pm$ 0.05	107.1 $\pm$ 21.8
<b>SHAM</b>	Overt	1	0.77 $\pm$ 0.12	131.6 $\pm$ 54.0	0.83 $\pm$ 0.08	94.0 $\pm$ 28.0
	Execution	2	0.77 $\pm$ 0.12	135.1 $\pm$ 56.1	0.85 $\pm$ 0.02	82.8 $\pm$ 19.7
<b>IPL</b>	Motor	1	0.77 $\pm$ 0.13	135.9 $\pm$ 48.7	0.79 $\pm$ 0.09	124.2 $\pm$ 38.2
	Imagery	2	0.77 $\pm$ 0.13	144.0 $\pm$ 58.6	0.78 $\pm$ 0.11	123.3 $\pm$ 33.0
<b>IPL</b>	Overt	1	0.76 $\pm$ 0.12	139.8 $\pm$ 57.3	0.83 $\pm$ 0.07	101.0 $\pm$ 32.7
	Execution	2	0.78 $\pm$ 0.09	139.6 $\pm$ 58.1	0.83 $\pm$ 0.06	96.9 $\pm$ 26.8
<b>SMA</b>	Motor	1	0.78 $\pm$ 0.13	137.6 $\pm$ 53.1	0.83 $\pm$ 0.03	108.2 $\pm$ 21.2
	Imagery	2	0.78 $\pm$ 0.09	142.7 $\pm$ 59.6	0.84 $\pm$ 0.03	108.5 $\pm$ 20.9
<b>SMA</b>	Overt	1	0.77 $\pm$ 0.13	131.8 $\pm$ 53.1	0.84 $\pm$ 0.05	92.7 $\pm$ 23.0
	Execution	2	0.78 $\pm$ 0.12	134.8 $\pm$ 60.3	0.84 $\pm$ 0.05	88.8 $\pm$ 19.6
<b>M1</b>	Motor	1	0.78 $\pm$ 0.13	131.0 $\pm$ 56.6	0.83 $\pm$ 0.06	105.2 $\pm$ 26.9
	Imagery	2	0.78 $\pm$ 0.10	134.0 $\pm$ 52.1	0.83 $\pm$ 0.06	97.7 $\pm$ 25.1
<b>M1</b>	Overt	1	0.76 $\pm$ 0.11	140.1 $\pm$ 61.4	0.82 $\pm$ 0.06	104.1 $\pm$ 25.0
	Execution	2	0.76 $\pm$ 0.10	135.2 $\pm$ 50.9	0.83 $\pm$ 0.04	99.3 $\pm$ 22.0



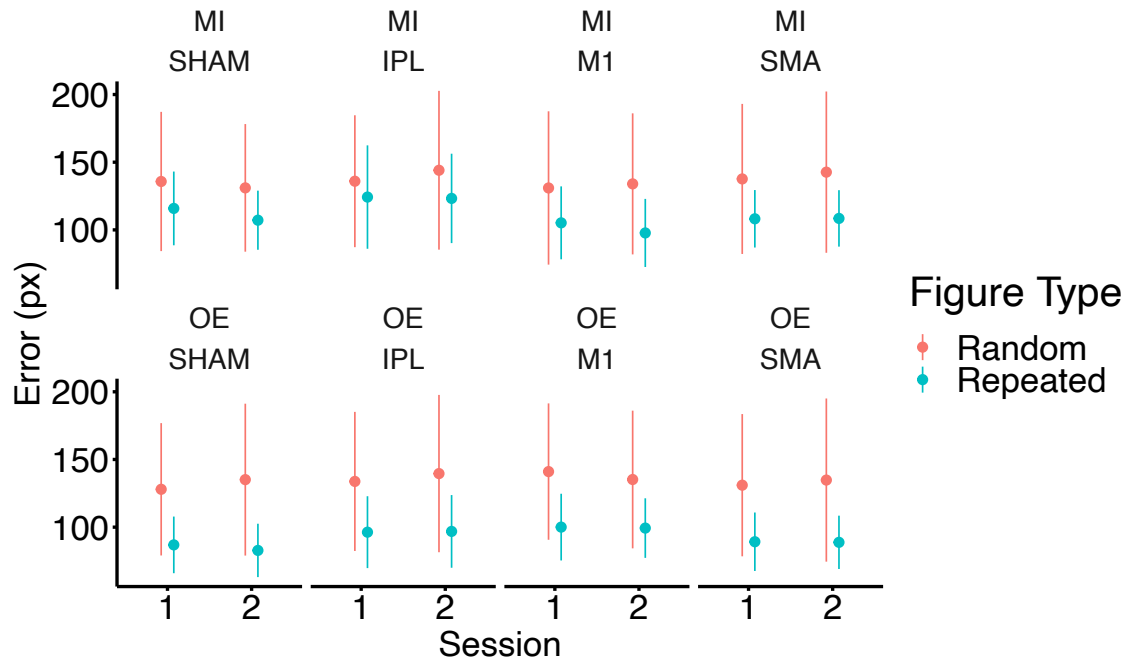


Figure 4.2: Mean error on each experimental session across stimulation site (columns) and practice modality (rows). Accuracy on the random trajectories is denoted by the red series and accuracy on the repeated trajectories is denoted by the blue series. All means are reported  $\pm$ SD

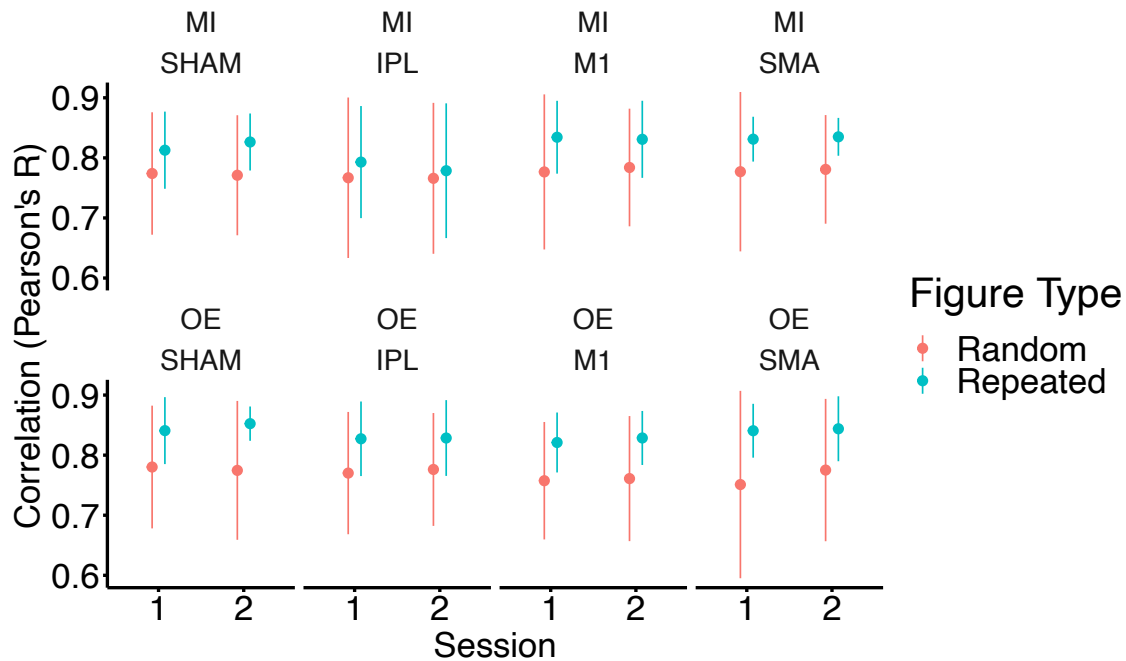


Figure 4.3: Mean turn angle correlation on each experimental session across stimulation site (columns) and practice modality (rows). Performance on the random trajectories is denoted by the red series and performance on the repeated trajectories is denoted by the blue series. All means are reported  $\pm$ SD

#### 4.4.2 Error:

The model predicting error revealed 14 credible and probable effects (Table 4.3). Of these effects, two main effects and two higher order interactions can explain the different combinations of predictors in this model: A) Stimulation Site<sub>[L\_IPL-SHAM]</sub> (Figure 4.4), B) Complexity (Figure 4.5), C) Stimulation Site<sub>[M1-SHAM]</sub> : Practice Modality : Session : Figure Type : Stimulus Animation Velocity (Figure 4.6) and D) Stimulation Site<sub>[SMA-SHAM]</sub> : Practice Modality : Session : Figure Type : Stimulus Animation Velocity (Figure 4.7). The main effect of stimulation to the L\_IPL demonstrates that stimulation impairs the accuracy of participant responses (Figure 4.4). The main effect of complexity demonstrates that increased stimulus complexity leads to less accurate participant responses (Figure 4.5). The M1 and SHAM stimulation site contrast, practice modality, session, figure type and stimulus animation velocity shows an effect, whereby stimulation to M1 impairs accuracy on all trajectories after overt execution practice but facilitates higher accuracy in the MI condition, especially on the repeated trajectory (Figure 4.6A). This effect leads to a decreased degree of learning on session 2 after overt execution practice and a facilitation of learning in both sessions after motor imagery practice (Figure 4.6B). In motor imagery this learning effect is largest on quickly animated trajectories in session 1 and slowly animated trajectories on session 2 (Figure 4.6B). The final interaction of the SMA and SHAM stimulation site contrast, practice modality, session, figure type and stimulus animation velocity reveal that the stimulation slightly impairs accuracy after overtly practicing the skill, except on slowly drawn trajectories in session 2, but minimally impacts learning on the task in this modality (Figure 4.7A and B). In motor imagery practice, the largest effect of stimulation to the SMA is facilitated accuracy of the repeated trajectory in session one which disappears in

session 2 (Figure 4.7A). This suggests that the improved accuracy resulting from stimulation to the SMA is realized in the first session, in contrast to the SHAM condition where accuracy of participant responses is aided by consolidation of the skill from session 1 to 2 (Figure 4.7B).

*Table 4.3: Summary of the posterior distribution for credible effects derived from Equation 4.1, predicting error. Each effect is denoted with a median beta value and an associated 89% highest posterior density interval (HPDI), the maximum probability of effect (MPE) and region of practical equivalence (ROPE).*

<b>Parameter</b>	<b>Median</b>	<b>MPE</b>	<b>ROPE</b>
Stimulation Site <sub>[L_IPL-SHAM]</sub>	0.26 [0.10:0.42]	0.99	0.03
Practice Modality	0.25 [0.15:0.34]	1	0
Figure Type	0.98 [0.92:1.05]	1	0
Stimulus Animation Velocity	0.28 [0.26:0.30]	1	0
Complexity	0.23 [0.21:0.25]	1	0
Stimulation Site <sub>[M1-SHAM]</sub> : Practice Modality	-0.54 [-0.86:-0.23]	1	0
Practice Modality : Figure Type	-0.46 [-0.57:-0.34]	1	0
Figure Type : Stimulus Animation Velocity	0.31 [0.27:0.35]	1	0
Stimulation Site <sub>[M1-SHAM]</sub> : Practice Modality: Figure Type	0.60 [0.20:1.00]	0.99	0
Stimulation Site <sub>[SMA-SHAM]</sub> : Figure Type : Stimulus Animation Velocity	0.22 [0.08:0.37]	0.99	0.06
Stimulation Site <sub>[M1-SHAM]</sub> : Practice Modality : Session : Figure Type	-0.57 [-1.08:-0.05]	0.96	0.05
Stimulation Site <sub>[M1-SHAM]</sub> : Session : Figure Type : Stimulus Animation Velocity	0.38 [0.14:0.62]	0.99	0.01
Stimulation Site <sub>[M1-SHAM]</sub> : Practice Modality : Session : Figure Type : Stimulus Animation Velocity	0.47 [-0.01:.096]	0.94	0.08
Stimulation Site <sub>[SMA-SHAM]</sub> : Practice Modality : Session : Figure Type : Stimulus Animation Velocity	0.45 [-0.03:0.94]	0.93	0.10

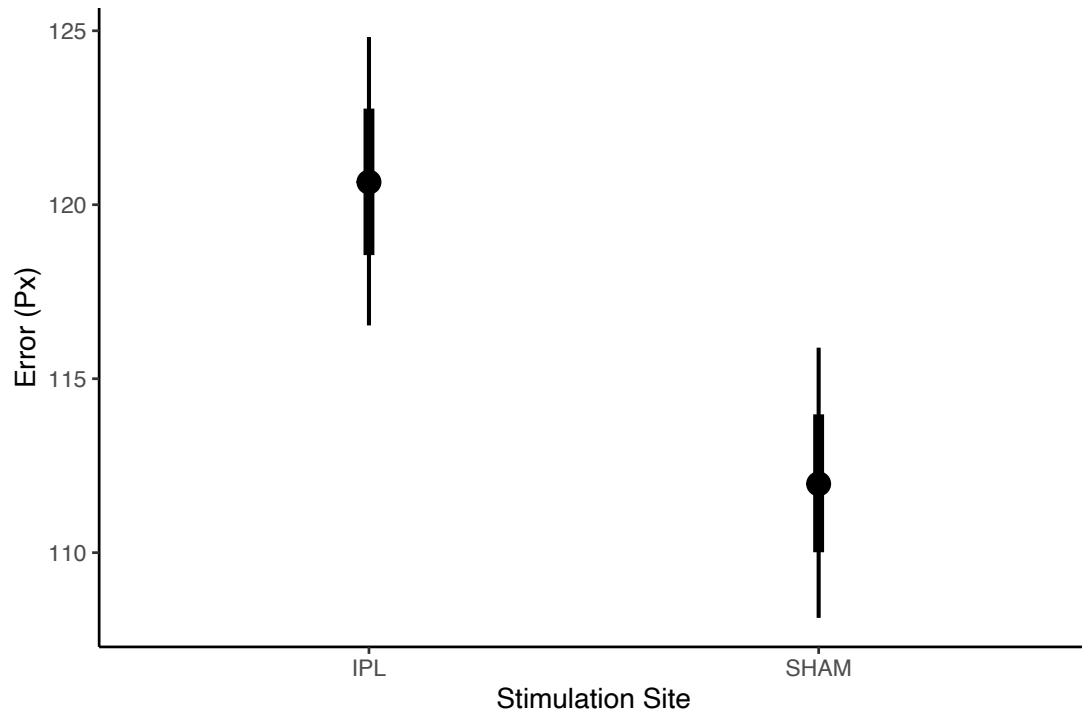


Figure 4.4: Median error attained after participants received SHAM stimulation or repetitive TMS to their left IPL. The thick and thin error bars represent the 60<sup>th</sup> and 90<sup>th</sup> quantiles respectively.

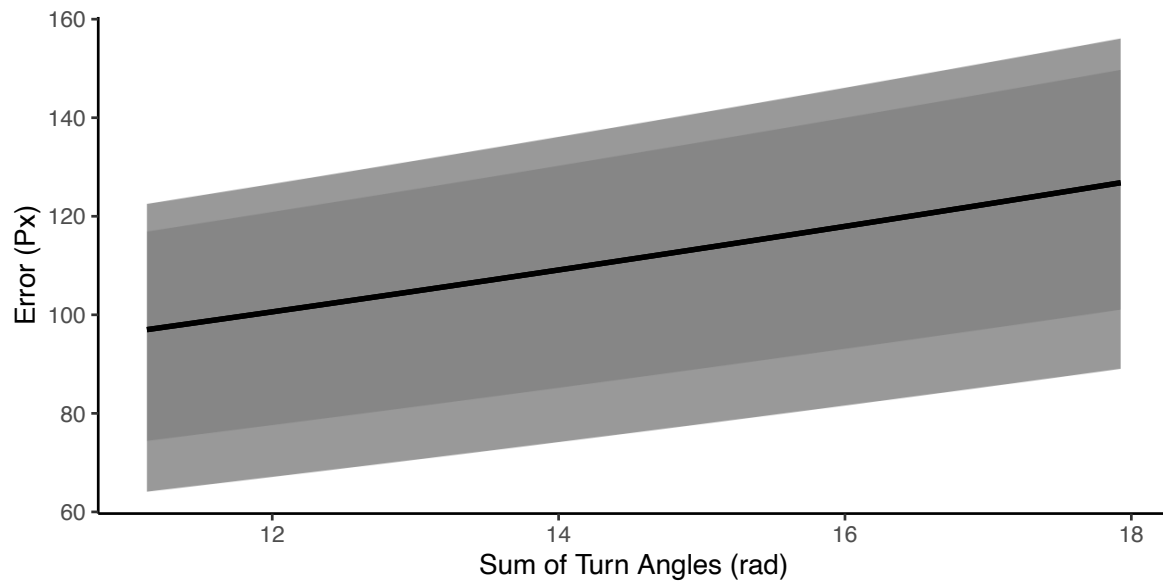


Figure 4.5: Median error attained across the 10<sup>th</sup> to 90<sup>th</sup> quantiles of the sum of turn angles (complexity) of a trial. The dark and light ribbons represent the 60<sup>th</sup> and 90<sup>th</sup> quantiles respectively.

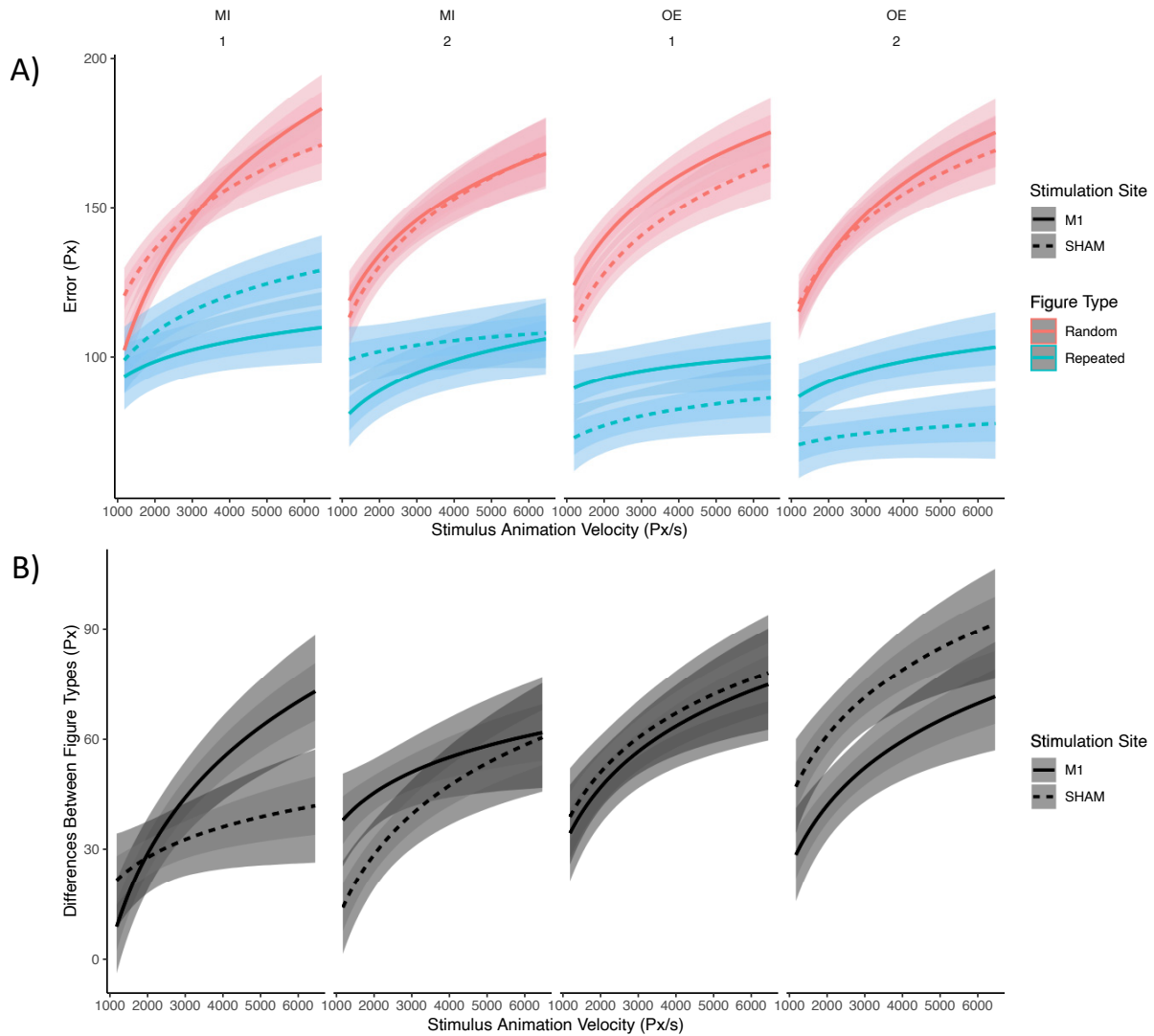


Figure 4.6: Median error attained across the 10<sup>th</sup> to 90<sup>th</sup> quantiles of stimulus animation velocity of a trial. Each subplot is a facet of practice modality and session. In A) the red series represents accuracy on random trajectories and the blue series denotes accuracy on the repeated trajectory. The solid line indicates accuracy of participants who received stimulation to their M1, and the dashed line represents the accuracy of SHAM participants. The dark and light ribbons represent the 60<sup>th</sup> and 90<sup>th</sup> quantiles respectively. In B) the relative difference between the two figure types is calculated from the red and blue series in A. The layout of the visualization is otherwise consistent.

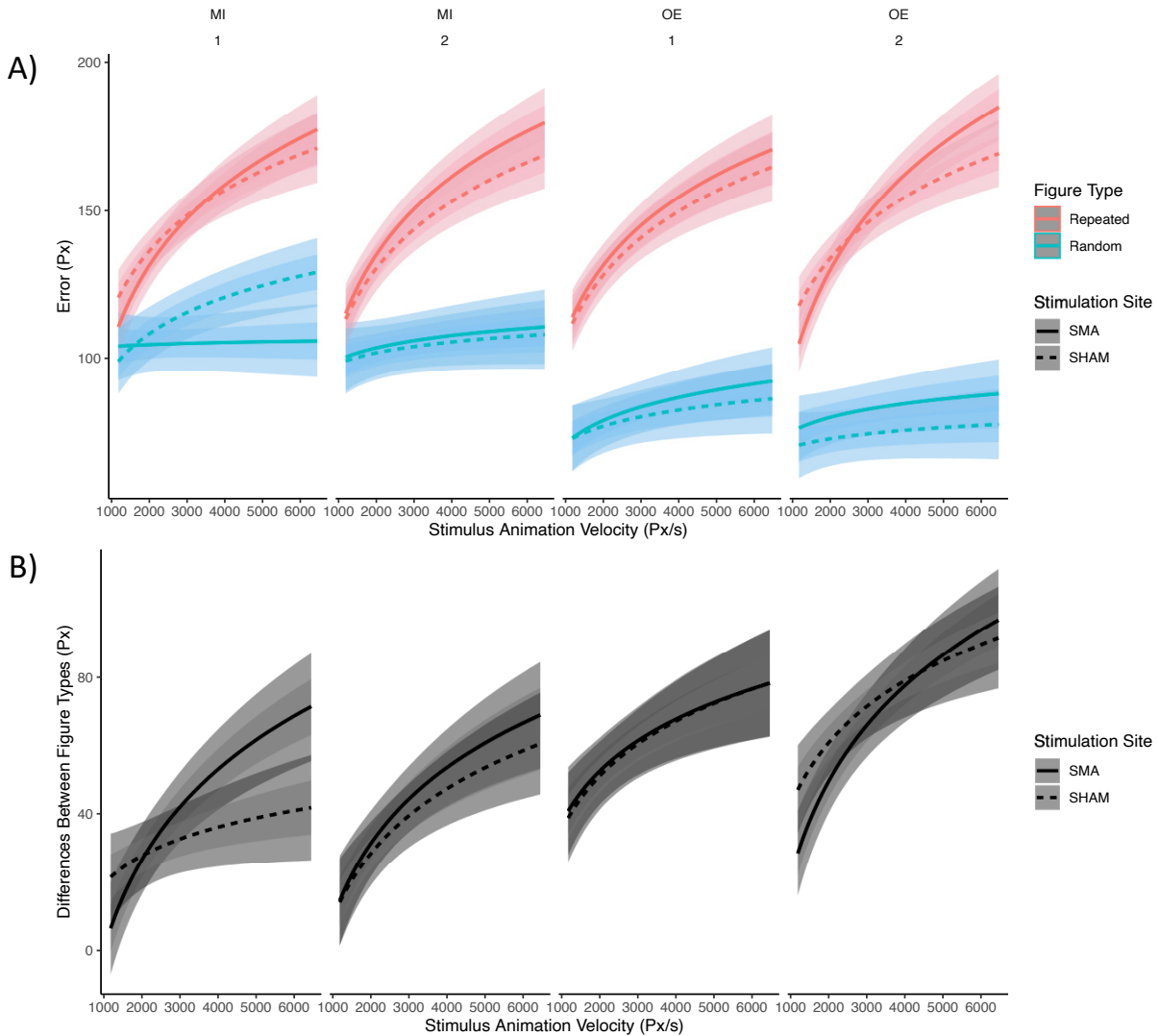


Figure 4.7: Median error attained across the 10<sup>th</sup> to 90<sup>th</sup> quantiles of stimulus animation velocity of a trial. Each subplot is a facet of practice modality and session. In A) the red series represents accuracy on random trajectories and the blue series denotes accuracy on the repeated trajectory. The solid line indicates accuracy of participants who received repetitive TMS to their SMA and the dashed line represents the accuracy of SHAM participants. The dark and light ribbons represent the 60<sup>th</sup> and 90<sup>th</sup> quantiles respectively. In B) the relative difference between the two figure types is calculated from the red and blue series in Figure A. The layout of the visualization is otherwise consistent.

#### 4.4.3 Correlations:

The model predicting turn angle correlations revealed 12 credible and probable effects (Table 4.4). Of these effects, 1 main effect and 3 higher order interactions can explain the different combinations of predictors in this model which will be visualized in turn. The main

effect of complexity demonstrates that as the stimuli become increasingly complex, the turn angle correlation between stimulus and response decreases (Figure 4.8). The first interaction denotes an effect of stimulation delivered to the M1 as it interacts with practice modality. In this interaction, stimulation to the M1 prior to motor imagery practice improves the correlations between stimulus and response whereas stimulation to the M1 prior to overt execution practice impairs the attained correlations (Figure 4.9). The final two interactions involve each predictor in the linear model and stimulation site contrast between the SMA and SHAM and L\_IPL and SHAM groups respectively (Figures 4.10 and 4.11). The interaction containing the SMA to SHAM stimulation suggests that in stimulation prior to motor imagery practice facilitates the turn angle correlations of both repeated and random trajectories, but the effect is most noticeable on repeated trajectories in session 1 and random trajectories in session 2 (Figure 4.10A). As a result, it appears that learning is facilitated in session 1 in this condition but impairs the consolidation process, largely driven by improvements on the random trajectory in session 2 (Figure 4.10B). In the overt execution practice modality, stimulation to the SMA impairs turn angle correlations on random trajectories in session 1, leading to a larger learning effect in that session (Figure 4.10A and B). The credible effect containing each predictor and the L\_IPL and SHAM stimulation site contrast reveals that stimulation to the L\_IPL impairs turn angle correlations in motor imagery, except on random trajectories in session 1, and is most noticeable on repeated trajectories in session 2 (Figure 4.11A). This suggests that stimulation to the L\_IPL impaired learning on this task (Figure 4.11B). After overt execution practice, stimulation to the L\_IPL also inhibited turn angle correlations, except on random trajectories in session 2 where the stimulation improved the attained correlations on rapidly animated stimuli

(Figure 4.11A). This effect suggests that the L\_IPL stimulation impairs learning on session 2

(Figure 4.11B).

*Table 4.4: Summary of the posterior distribution for credible effects derived from Equation 4.2, predicting turn angle correlations. Each effect is denoted with a median beta value and an associated 89% highest posterior density interval (HPDI), the maximum probability of effect (MPE) and region of practical equivalence (ROPE).*

Parameter	Median	MPE	ROPE
Stimulation Site <sub>[L_IPL-SHAM]</sub>	-0.24 [-0.42:-0.05]	0.98	0.1
Figure Type	-0.70 [-0.77:-0.63]	1.00	0
Complexity	-0.13 [-.15:-0.10]	1.00	0.02
Stimulation Site <sub>[M1-SHAM]</sub> : Practice Modality	0.42 [0.07:0.78]	0.97	0.05
Stimulation Site <sub>[L_IPL-SHAM]</sub> : Practice Modality	-0.43 [-0.80:-0.07]	0.97	0.05
Stimulation Site <sub>[L_IPL-SHAM]</sub> : Figure Type	0.39 [0.16:0.61]	1.00	0
Practice Modality : Figure Type	0.29 [0.15:0.42]	1.00	0
Figure Type : Stimulus Animation Velocity	-0.14 [-0.19:-0.09]	1.00	0.08
Stimulation Site <sub>[L_IPL-SHAM]</sub> : Practice Modality : Session : Stimulus Animation Velocity	0.46 [0.11:0.80]	0.98	0.02
Stimulation Site <sub>[SMA-SHAM]</sub> : Session : Figure Type : Stimulus Animation Velocity	-0.41 [-0.78:-0.05]	0.96	0.06
Stimulation Site <sub>[SMA-SHAM]</sub> : Session Structure : Session : Figure Type : Stimulus Animation Velocity	-0.61 [-1.30:-0.11]	0.92	0.07
Stimulation Site <sub>[L_IPL-SHAM]</sub> : Session Structure : Session : Figure Type : Stimulus Animation Velocity	1.13 [0.42:1.84]	0.99	0



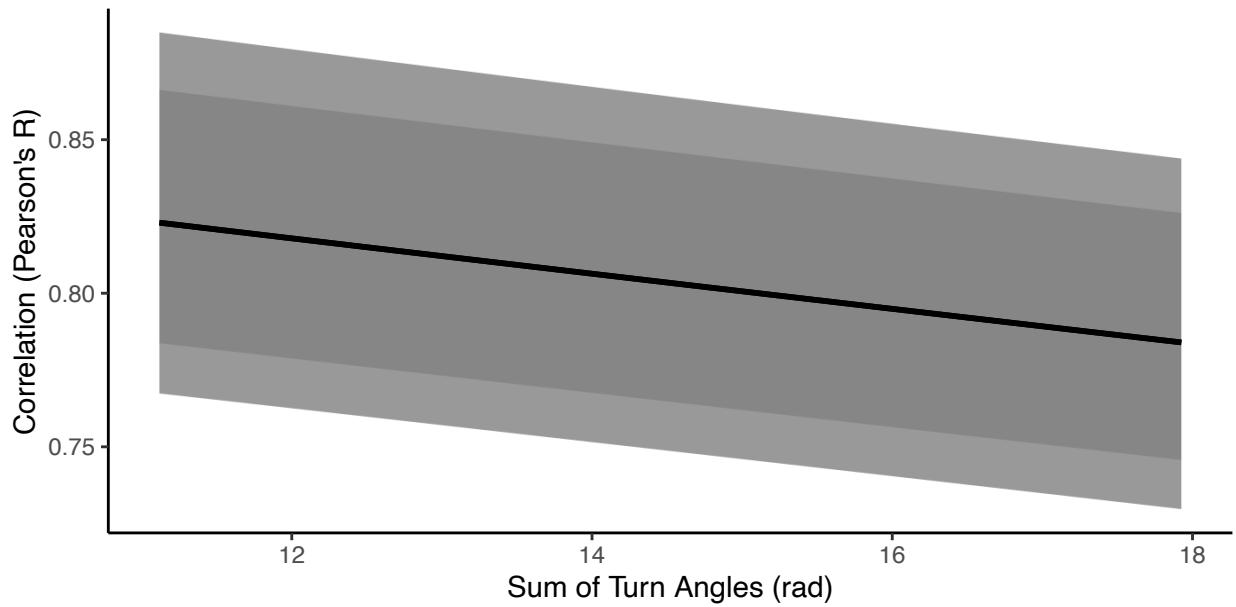


Figure 4.8: Median turn angle correlation attained across the 10<sup>th</sup> to 90<sup>th</sup> quantiles of the sum of turn angles (complexity) of a trial. The dark and light ribbons represent the 60<sup>th</sup> and 90<sup>th</sup> quantiles respectively.

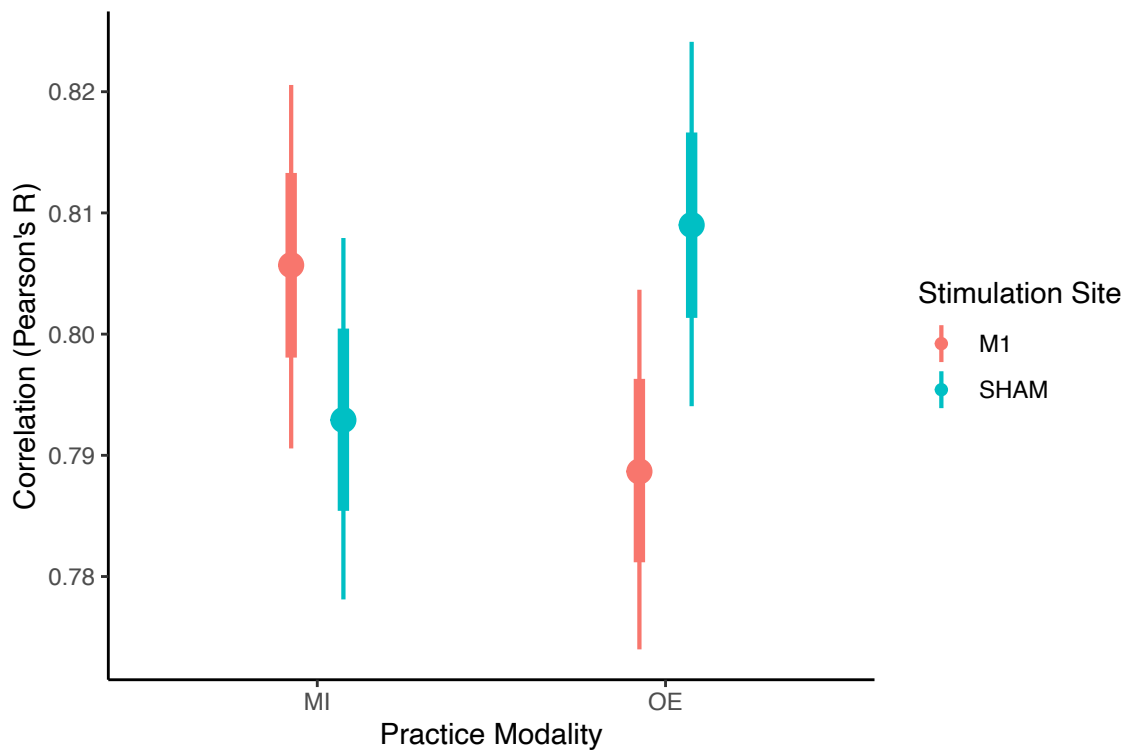


Figure 4.9: Median turn angle correlation after receiving SHAM stimulation (blue) or repetitive TMS delivered to the M1 (red) separated by practice modality (overt execution [OE] and motor imagery [MI]). The thick and thin error bars represent the 60<sup>th</sup> and 90<sup>th</sup> quantiles respectively.

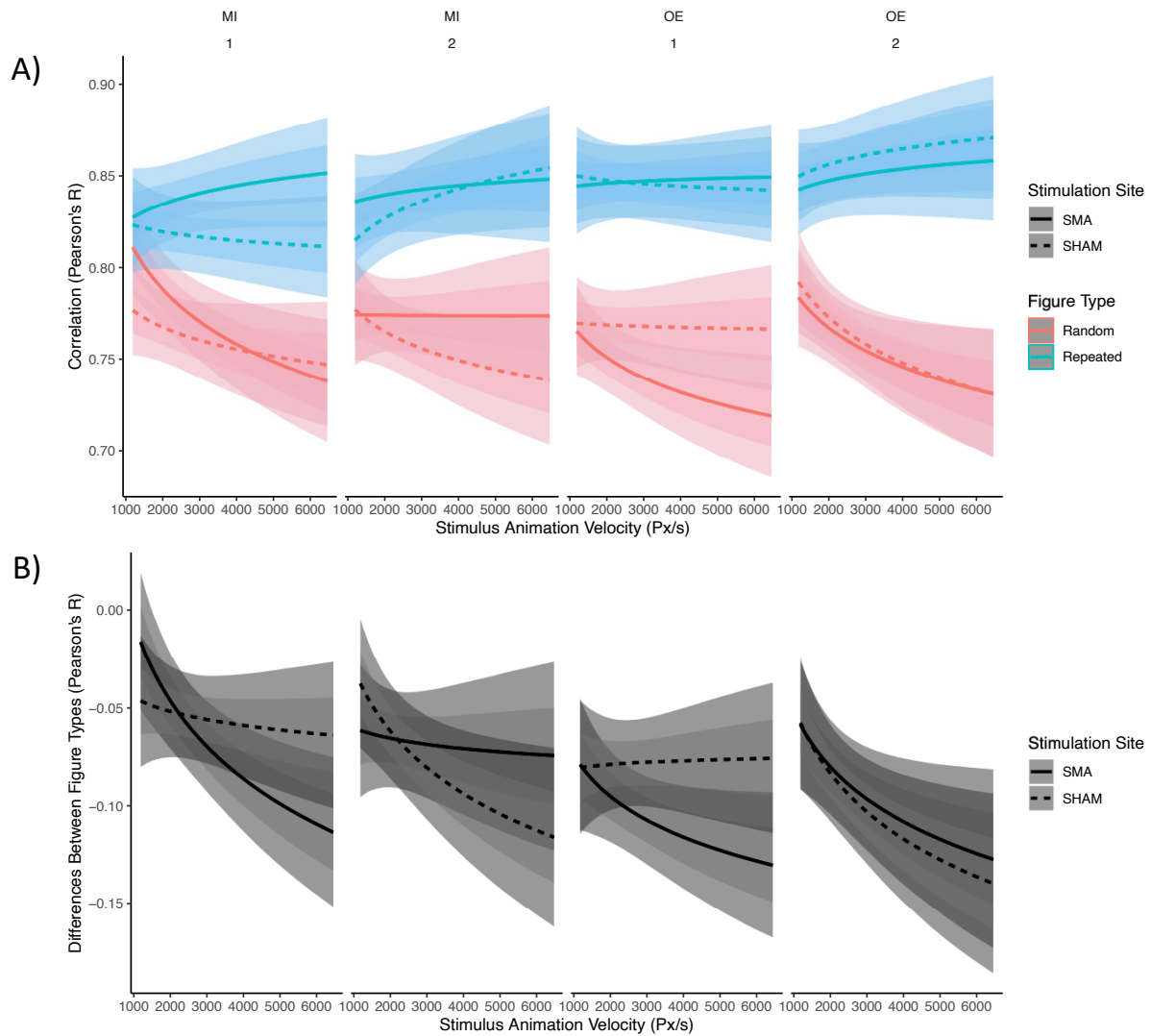


Figure 4.10: Median turn angle correlations attained across the 10<sup>th</sup> to 90<sup>th</sup> quantiles of stimulus animation velocity of a trial. Each subplot is a facet of practice modality and session. In A) the red series represents performance on random trajectories and the blue series denotes performance on the repeated trajectory. The solid line indicates performance of participants who received stimulation to their SMA, and the dashed line represents the performance of SHAM participants. The dark and light ribbons represent the 60<sup>th</sup> and 90<sup>th</sup> quantiles respectively. In B) the relative difference between the two figure types is calculated from the red and blue series in A. The layout of the visualization is otherwise consistent.

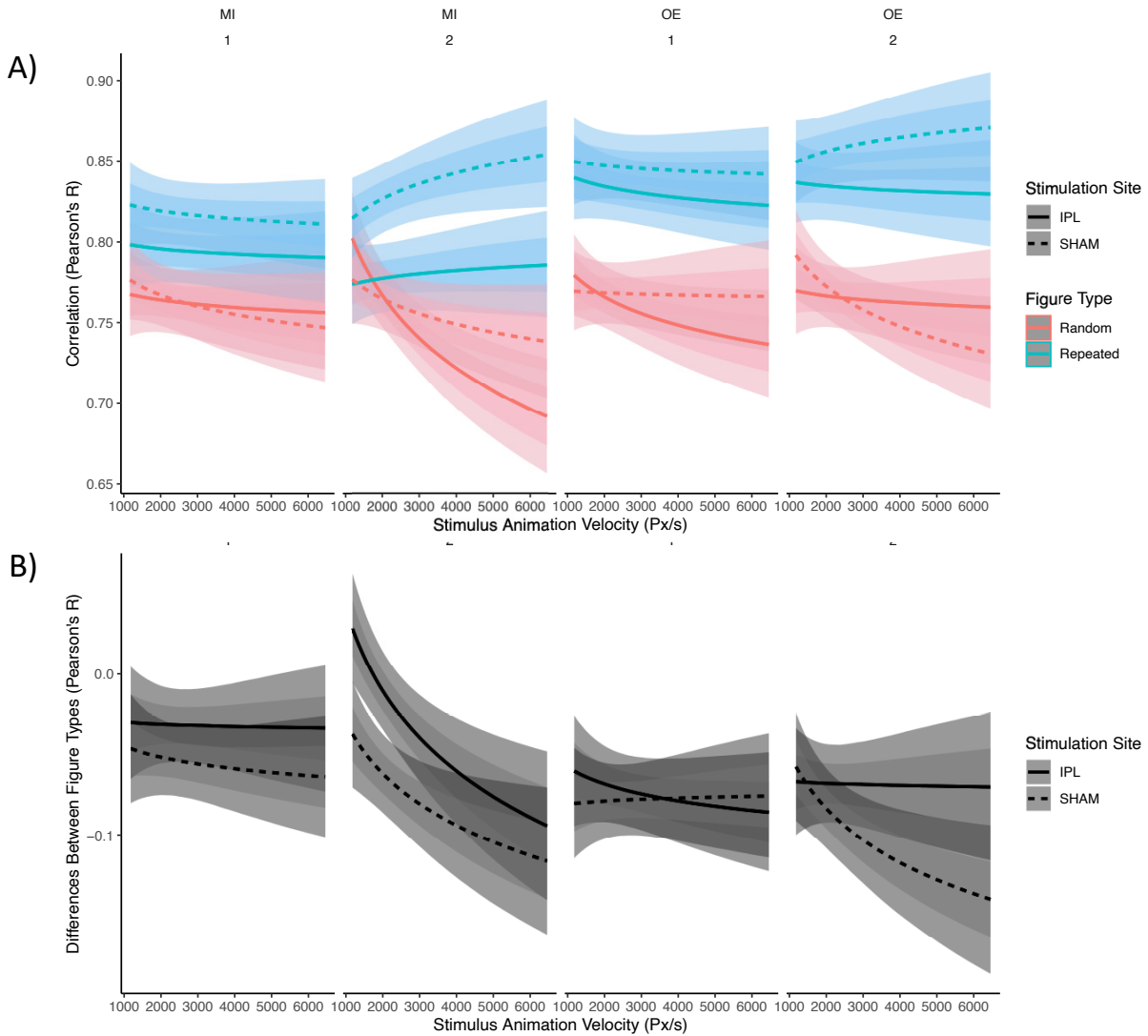


Figure 4.11: Median turn angle correlations attained across the 10<sup>th</sup> to 90<sup>th</sup> quantiles of stimulus animation velocity of a trial. Each subplot is a facet of practice modality and session. In A) the red series represents performance on random trajectories and the blue series denotes performance on the repeated trajectory. The solid line indicates performance of participants who received stimulation to their L\_IPL and the dashed line represents the performance of SHAM participants. The dark and light ribbons represent the 60<sup>th</sup> and 90<sup>th</sup> quantiles respectively. In B) the visualized relative difference between the two figure types is calculated from the red and blue series in A. The layout of the visualization is otherwise consistent.

#### 4.5 Discussion:

The purpose of this study was to replicate early findings of the effects of repetitive TMS on motor imagery-based motor learning using a kinematically complex task to determine if the task used impacted contemporary views of the nature of motor imagery (S. N. Kraeutner, Keeler,

et al., 2016; S. N. Kraeutner, Ingram, et al., 2017; Solomon et al., 2021). In the original series of studies, it was found that repetitive TMS applied to the L\_IPL before motor imagery training impaired motor imagery-based motor learning to a greater degree than overt execution, and further that stimulation to the M1 did not affect motor imagery-based motor learning. Finally, transient inhibition of the SMA affected stimulus response mapping in imagery but not overt execution of the SRTT-like paradigm used (S. N. Kraeutner, Keeler, et al., 2016; S. N. Kraeutner, Ingram, et al., 2017; Solomon et al., 2021). In this experiment we replicate the experimental manipulation whereby repetitive TMS was applied to the same three regions (i.e., the L\_IPL, M1 and SMA) prior to engaging in a multi-articular trajectory production task (T. G. J. Ingram et al., 2019). Be it that the purpose of the study was replication in a different task, the hypotheses made aligned with the published findings. Treating each tested region as a separate hypothesis largely revealed a replication of the findings for stimulation to the L\_IPL but not for the M1 or SMA. Repetitive TMS delivered to the L\_IPL impaired accuracy similarly across all experimental variables as evidenced by the main effect of the stimulation site contrast between the L\_IPL and SHAM groups (Figure 4.4). In overt execution this finding is supported by a uniform decrease in turn angle correlation across the repeated trajectory (Figure 4.11A). In motor imagery, there is a large drop in the turn angle correlation on the repeated trajectory from session 1 to 2 suggesting that the stimulation negatively impacted the consolidation of the control policy governing movement (Figure 4.11A and B). These findings indicate that stimulation seems to impair performance in both conditions and has a larger impact on consolidation, loosely aligning with conclusions from Kraeutner et al., (2016). Stimulation to the M1 impaired accuracy and reduced turn angle correlations on the task and limited consolidation of the learned skill in

overt execution but in imagery this trend is inverted and stimulation to the M1 improved the accuracy of the repeated trajectory, facilitating learning (Figure 4.6 and 9). This finding is interesting as it suggests that uninhibited function of the M1 impairs motor imagery-based motor learning in this task (see section 4.5.3 Impact of task and considerations for future research below), contrasting findings of Kraeutner et al., (2017). Lastly, stimulation to the SMA inhibited the accuracy on the task in overt execution, whereas after motor imagery practice, stimulation to the SMA facilitated resulted in improved accuracy during session 1 (Figure 4.7A and B). These differences correspond with improved turn angle correlations in session 1 post imagery practice and impaired correlation on the random trajectories during session 1 after overt execution practice (Figure 4.10A and B).

#### 4.5.1 *Inferior Parietal Lobe:*

The IPL has been of particular interest to the field of motor imagery given its involvement in the cortical network underlying imagery, and in turn its probable importance to motor learning via motor imagery and its roles in state estimation and sensory integration for movement (Haar & Donchin, 2020; Hardwick et al., 2018; S. N. Kraeutner, Keeler, et al., 2016; Medendorp & Heed, 2019). These previous TMS findings in the motor imagery literature have led to the creation of multiple theories describing the behavioural mechanisms that are grounded in the concept that motor imagery relies on areas of the brain that support the covert components of movement control, goal, and action selection (Frank & Schack, 2017; Glover & Baran, 2017; Krakauer et al., 2019). However, the tasks used to generate these findings are relatively simple in nature and, as such, the bias towards the critical importance of the L\_IPL to motor imagery might arise because of the nature of the tasks used to study them. Results of this

study provide additional support for the belief that the functions subserved by the L\_IPL is crucial for motor imagery as repetitive TMS to the L\_IPL impaired skill acquisition in this kinematically complex motor task. Specifically, results from this study imply a role for the L\_IPL in motor learning of a generalized skill and, in motor imagery, the consolidation of a practiced movement. The main effect of stimulation to the L\_IPL supports the conclusion that the area is involved in generalized execution of the task in both modalities (Figure 4.4). However, by evaluating the correlations of turn angles between stimulus and participant responses, the degradation of accuracy is accompanied by a large drop in turn angle correlation in session 2 in motor imagery that is notably absent in overt execution (Figure 4.11A). The contrast between motor imagery and overt execution would suggest that in overt execution the degradation of performance is likely caused by errors in execution of the selected action, whereas in motor imagery inaccuracies in the consolidated control policy contributed to impaired performance on the task. This finding aligns with the previous conclusions Kraeutner et al., (2016) where inhibition of the L\_IPL impairs learning on a SRTT in imagery more than overt execution, further supporting the understanding that motor imagery-based motor learning relies on improvements to the covert components of movement, goal, and action selection (Frank & Schack, 2017).

However, the timing of the effect on turn angle correlation is noticeably different between the studies as the effects of stimulation on learning manifest by the end of the first and only session in the Kraeutner et al., (2016) study, whereas, in the current study, the effects of stimulation on learning appear in session 2. The differences in timing of this effect creates ambiguity around the role of the L\_IPL in motor imagery, which could speculatively be due to

the novelty of movement in the current task. Since drawing complex trajectories on a touch screen is not a well-practiced movement in comparison to pressing buttons on a keyboard, the control policy governing action execution in the current task would not be well established at the end of session 1. In contrast the control policy for button presses used in a SRTT would be well-established prior to the participants engaging in the paradigm. Given that stimulation to the L\_IPL demonstrated the largest impact on turn angle correlation in session 2, the region could therefore be involved in refining known control policies but may not be as vital in the formation of novel ones.

#### *4.5.2 Motor Cortex and Supplementary Motor Area:*

Unlike the L\_IPL, results attained after repetitive TMS delivered to the M1 contradicts the findings of past research in motor imagery but not in overt execution (S. N. Kraeutner, Ingram, et al., 2017; Krakauer et al., 2019). Stimulation to the M1 in overt execution was intended as a control condition to ensure that the stimulation was interfering with the area's known role in the consolidation of motor skills (Krakauer et al., 2019; Muellbacher et al., 2002; Richardson et al., 2006). Results from this study largely align with this theory as inhibition of M1 in overt execution impaired accuracy of both random and repeated trajectories and the corresponding turn angle correlations in overt execution, (Figure 4.6A and 9), and impaired consolidation of the learned skill where the magnitude of the difference between trajectory types was reduced in session 2 (Figure 4.6B). However, in motor imagery, stimulation to the area improved accuracy of participant responses to the repeated trajectory and improved the corresponding turn angle correlations, facilitating skill acquisition (Figure 4.6A and 9). This result contrasts against results from Kraeutner et al., (2017) whereby stimulation to the M1 did not

affect skill acquisition and further contrasts against earlier TMS studies targeting the M1 demonstrating impairments to motor imagery performance of a hand laterality judgment task (Pelgrims et al., 2011a). This complete spectrum of behavioural results is further contrasted against neuroimaging evidence that has found that the M1 is not active during motor imagery performance and therefore shouldn't play an active role in motor imagery-based motor learning (Hardwick et al., 2018; Kasess et al., 2007; Solomon et al., 2019b).

Results of stimulation to the SMA are also contrasting to results from the previous study using a SRTT-like paradigm. In this previous study, stimulation to the SMA impaired learning on the task in both overt execution and motor imagery by slowing reaction times to the repeated sequence to a greater extent than randomly generated cues (Solomon et al., 2021). In the current study this trend is inverted, whereby stimulation to the SMA improved the accuracy of participant responses to the repeated trajectory in session 1 after motor imagery practice (Figure 4.7A). These changes are associated with improvement of the turn angle correlations in session 1 as a result of stimulation (Figure 4.10A). Similarly, the results of SMA stimulation after overt execution are also in contrast with the previous results as the accuracy of responses to both trajectory types was impaired, indicating that the region seems to be involved in action execution of the task but doesn't seem to contribute to learning (Figure 4.7A and B). These changes in accuracy after overt execution practice were accompanied by decreasing similarity in turn angle correlations on random trajectories in session 1 that was not seen in session 2, indicating that the reduced accuracy on the task is likely a function of the SMA's involvement in action execution (Figure 4.10A and B). In summary, the effects of stimulation to the SMA seem



to mirror those of M1 stimulation whereby repetitive TMS to either area is facilitating performance in imagery and impairing performance in overt execution of complex trajectories.

#### *4.5.3 Impact of Task and Considerations for Future Research:*

Given the contrasting results from stimulation of the SMA and M1 and the additional confound of the lack of M1 involvement in motor imagery, the most plausible explanation for the lack of a repeatable outcome is that the tasks employed to investigate learning have differing demands on these regions of the cortex. For instance, the hand laterality judgement task, a task where participants identify if pictures of hands oriented at different directions are left or right hands, relies on implicit motor imagery which recruits a different neural network than conscious motor imagery performance (Hétu et al., 2013). Serial reaction time tasks only rely on the M1 to store and execute representations of the individual, discrete movements required to perform the task and the learned behaviour, and the ordering of these discrete actions is reliant on the premotor and parietal cortices (Schwarb & Schumacher, 2012; Wong & Krakauer, 2019; Yokoi & Diedrichsen, 2019). The current task has only been used once in conjunction with neuroimaging (in this instance electroencephalography) and a small magnitude of activity noted for the sensorimotor regions of the brain during motor imagery performance thought to be representative of the task's focus on action execution (T. G. J. Ingram, 2021). This finding provides some evidence to indicate that the M1 is involved in motor imagery of the task but fails to explain why it's inhibition would lead to facilitation of learning. Given the similarity between the results obtained after stimulation to the SMA and M1, it is likely that both of these regions are involved in a similar mechanism related to the complex movement execution paradigm. One hypothesis could be that the current task relies not only on

recalling the covert components of movement to perform imagery of the task but has additional demands on memory to maintain a representation of the stimulus. This memory function could be relying on areas of the sensorimotor region that are otherwise involved in motor imagery-based motor learning. As such, this could create a potential scenario where there is competition for neural resources in the sensorimotor region involving processes related to mapping the recalled stimulus to an associated, previously unperformed action that ends up limiting learning via motor imagery on the task. As such, when the M1 or SMA were inhibited, the conflict between behavioural processes is eliminated and learning on the task improves. Although this conclusion is purely conjecture, it would be easily testable by performing the experiment again but leaving the stimulus on screen during imagery performance to remove the memory demands of the task.

#### *4.6 Conclusions:*

Results of the current study support the previously established theory that motor imagery-based motor learning relies on the function of the L\_IPL and highlights a potential role for this area in the consolidation of the control policy for movement (S. N. Krautner, Keeler, et al., 2016). However, these suggestions are made in light of inconsistencies in the effects of stimulation to the SMA and M1 in comparison to past literature (S. N. Krautner, Ingram, et al., 2017; Solomon et al., 2021). These differences highlight an important realization that the nature of the task used likely has a large impact on results in the study of motor learning, particularly when the modality used for learning is motor imagery. In overt execution, the impact of task selection has been classified based on their contribution to different stages of motor control, but this mapping has yet to be investigated in the study of motor imagery (Krakauer et al.,

2019). One of the contributing factors to this problem is the lack of consensus as to the overlap between control of movement between overt execution and motor imagery (Frank & Schack, 2017; Hurst & Boe, 2022; O'Shea & Moran, 2017). As such, it is difficult to restrict the interpretation of results obtained from a specific task to components of motor learning in motor imagery. This scenario increases the probability of over generalizing one's findings from a single task to motor imagery as a modality. Rather, using a battery of tasks to investigate learning effects within participants would be an achievable alternative solution to mitigate the impact of task in the study of motor learning via motor imagery. Consistent findings across tasks would therefore be more likely to represent meaningful properties of the modality employed for training and in-turn learning. Applying this logic to the results obtained from this study highlights the reliance of motor imagery-based motor learning on the L\_IPL, in contrast to inconsistent findings resulting from stimulation to the SMA and M1 which may reflect effects specific to the employed paradigm.

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## Chapter 5: DISCUSSION

### 5.1 *Purpose:*

The overall objective of this thesis was to address methodological limitations of previous investigations of motor imagery probing the role of the inferior parietal lobes (IPL) and explore the possibility that task selection is impacting the generalizability of the findings. The IPLs have notable importance to motor imagery based on their consistent involvement in the neural network underlying its performance, and the consistent finding that inhibitory stimulation to the left inferior parietal lobe (L\_IPL) impairs motor imagery-based motor learning more so than overt execution (Hardwick et al., 2018; S. N. Kraeutner, Keeler, et al., 2016). However, the use of repetitive TMS in Kraeutner et al., (2016) caused a lasting inhibitory effect on the cortex (approximately 45-60 minutes) and, as such, the importance of the L\_IPL to motor imagery could be gleaned but not its role in a specific mechanism (Huang et al., 2005). Additionally, like many past investigations of the contributions of cortical regions to motor imagery, the Kraeutner et al., (2016) study used a kinematically simple paradigm to investigate motor learning as driven by motor imagery (Hardwick et al., 2018; Puce & Hämäläinen, 2017). A consequence of this decision is that the SRT-like task used doesn't rely on all components of motor control (see section 4.2 Introduction for details) but rather emphasizes the goal and action selection components (Krakauer et al., 2019). As such, it is possible that task selection influenced conclusions drawn from the study and is contributing to the belief that motor imagery-based motor learning relies on improvements to goal and action selection (rather than execution) to drive learning (Figure 1.2; Frank et al., 2023; Krakauer et al., 2019). To address these issues, this thesis investigates the role of the L\_IPL using different TMS approaches before

or during performance of a complex movement execution task that emphasizes action execution to drive learning (Huang et al., 2005; T. G. J. Ingram et al., 2019; Prime et al., 2008). The first study in this thesis used a temporally constrained single pulse TMS paradigm to test a specific role of the L\_IPL in the provision of simulated feedback that would permit the detection of errors resulting from motor imagery performance (Figure 1.7; Dahm & Rieger, 2019b; Prime et al., 2008). The second study explored improvements to the data and statistical analysis approaches used to investigate motor learning via motor imagery using the complex movement execution paradigm and introduced a correlation-based outcome measure to represent the similarity between the stimulus and participant response that is thought to be representative of the control policy governing the movement. Lastly, the third chapter replicated a series of studies using repetitive TMS to investigate the effects of inhibition on different cortical regions important to motor learning, including the L\_IPL, using the complex movement trajectory task to measure the impact of task selection on conclusions made about the nature of motor imagery-based learning (Huang et al., 2005; S. N. Kraeutner, Keeler, et al., 2016; S. N. Kraeutner, Ingram, et al., 2017; Solomon et al., 2021). The results of each study will be summarized sequentially in the following section before discussing the role of the L\_IPL in more detail and discussing the impact of task selection in the study of motor imagery.

## *5.2 Summary of empirical chapters:*

### *5.2.1 Chapter 2:*

In this chapter, single pulse TMS was delivered 100ms after each trial of a complex movement execution task to interrupt the L\_IPL's proposed function of providing simulated feedback during motor imagery. Specifically, the theory for learning via motor imagery proposed

by Dahm and Rieger, 2019 (Figure 1.7) lacks a clear mechanism to describe how errors are generated in motor imagery. In this chapter we proposed an alternative mechanism for imagery that relies on a simulation of the observed effects of movement and suggested that the IPL was involved in the comparison of this simulation against the intended effect of movement (Figure 2.1C). The study showed no effects of stimulation. Given the multitude of findings in the literature denoting the importance or involvement of the area in motor imagery, this null finding was likely to be a function of the timing of the stimulation or that the prescribed function of the L\_IPL's involvement in motor imagery was incorrect (Solomon et al., 2022). Stemming from this study, the question of task effects was brought forward as potential contributors to the differences between the obtained results and the past literature. As such, the focus of the following chapters pivoted away from the role of the L\_IPL and focused on establishing consistent conclusions across tasks in the motor imagery literature.

### 5.2.2 Chapter 3:

The first step in evaluating task related effects in the literature was to establish confidence in the measures used to quantify learning in the complex movement execution task used across each study in this thesis (T. G. J. Ingram et al., 2019). The purpose of the analysis employed in Ingram et al., (2019) for the complex movement execution task was to help compensate for the variable speed of the participant responses and differences in the execution of the responses in comparison to the stimuli. The result was theoretically an error-based measure that should represent improvements to the control policy to govern movement ignoring errors in execution of the response, including inappropriate scaling, rotation, or translation. This chapter re-analyzes the data collected by Ingram et al., 2019 using a new

analysis approach that improved the process of controlling for the variable speed of participant responses by using interpolation functions rather than DTW. Subsequently, DTW is applied to the turn angles between consecutive samples to accurately compare the stimulus and response on a given trial. The novel analysis overcame a variety of limitations of the original analysis (Figure 3.2A-C) and importantly only minimally affected the conclusions drawn from each analysis approach. Additionally, a new correlation-based outcome measure, turn angle correlation, was introduced as what we considered to be a better measure of the control policy governing movement as turn angle correlation is unaffected by issues believed to be resulting from action execution: scaling, rotation, and translation. An analysis of this novel measure revealed improvements of motor imagery and physical practice training in comparison to the perceptual control group on the control policy governing movement. These findings were consistent with those of the original analysis by Ingram et al., (2019). With this updated analysis approach and new outcome measure, a reproduction of earlier investigations of the involvement of different cortical regions in motor imagery-based motor learning was conducted to determine if task selection was biasing which cortical regions were found to be important for task performance.

### 5.2.3 Chapter 4:

This study sought to determine if task selection was biasing the interpretation of results from the study of the importance of different cortical regions to motor imagery. To achieve this goal, the study attempted to replicate the findings of an earlier series of studies using repetitive TMS to inhibit the L\_IPL, M1 or SMA prior to learning a series of button presses in a SRT-like task (S. N. Kraeutner, Keeler, et al., 2016; S. N. Kraeutner, Ingram, et al., 2017; Solomon et al., 2021).

The study reported in Chapter 4 used the same TMS paradigm and cortical targets but used the complex movement execution task instead of the SRT-like task. The intent here was to use a task that emphasized action execution through the use of a continuous, novel, multi-joint movement as opposed to goal selection and action planning components of movement control. Results from each cortical region targeted were considered separately and revealed partial replication of the previous findings. Namely, we found an effect of stimulation to the L\_IPL consistent with prior work, but dissimilar findings for the M1 and SMA. Stimulation to the L\_IPL decreased accuracy of the participant responses and was associated with impaired consolidation of the control policy in motor imagery but not in execution. This finding suggests that motor imagery relies on function of the L\_IPL for learning aligning with past literature (S. N. Kraeutner, Keeler, et al., 2016). However, the results from stimulation to the M1 and SMA are in stark contrast to previous literature: where the current results suggest that the stimulation facilitated performance of the skill when learned via imagery and impaired performance when training using overt execution (S. N. Kraeutner, Ingram, et al., 2017; Pelgrims et al., 2011b; Solomon et al., 2021). The effects of M1 stimulation are especially surprising given the noted lack of involvement of this region in the neural network underlying motor imagery performance (Hardwick et al., 2018). These conflicting results are likely a product of a noted task related bias in the neuroimaging literature as previous electroencephalography investigations of this task have demonstrated recruitment of the sensorimotor cortex involvement during imagery (Hardwick et al., 2018; T. G. J. Ingram, 2021). Likewise, the lack of M1 involvement noted in the previous literature could be due to the kinematic simplicity of the tasks used. As an example, activity in the M1 recorded during SRTTs is only reflective of single, previously known elements

and the learned behaviour, the ordering of these elements, is represented widely across the cortex (Wong & Krakauer, 2019; Yokoi & Diedrichsen, 2019). The direction of the stimulation effects is also surprising as it suggests that in this task, unaffected function of the M1 and SMA are limiting the rate of learning in the complex movement execution task. It is possible that this task specifically could be involved in a separate cognitive process that has to recall the stimulus on a trial from memory before integrating it into the planning process which could result in interference that limits motor imagery-based motor learning. However, the most valuable conclusion from this study is that motor imagery continues to rely on the function of the L\_IPL to drive learning as this effect generalizes across tasks in contrast to stimulation at the other targets of interest.

### *5.3 The role of the left inferior parietal lobe in motor imagery:*

The primary contribution of this thesis to the understanding of the nature of motor imagery is that the L\_IPL is vital to the network underlying imagery. This result was a replication of prior work obtained largely from kinematically simple movements and supports the generalization of this finding to motor imagery (Burianová et al., 2013; Hardwick et al., 2018; Héту et al., 2013; S. Kraeutner et al., 2014; S. N. Kraeutner, Keeler, et al., 2016). In overt execution, the parietal lobes are proposed to be involved in representing movement within the construct of the task (Haar & Donchin, 2020). The area's role in creating these movement to state relationships has been evidenced through a variety of potential functions including sensorimotor integration for visually guided movements, state estimation in optimal feedback control, high-order sensorimotor information integration and conscious motor intentions (Buneo & Andersen, 2006; Desmurget & Sirigu, 2012; Fogassi & Luppino, 2005; Shadmehr &

Krakauer, 2008; Wolpert & Ghahramani, 2000). Based on these functions, the wealth of neuroimaging and TMS investigations of the L\_IPL in motor imagery has concluded that motor imagery relies on these associated functions and is therefore biased towards these perceptual components of motor control, although the exact role of the L\_IPL in motor imagery is still debated (Hardwick et al., 2018; S. N. Kraeutner, Keeler, et al., 2016).

Given the role of the parietal lobes in creating movement to state relationships and the L\_IPL's involvement in the networks underlying motor imagery, the L\_IPL could be involved in the process of simulating the overt effects of movement (see Chapter 2: Introduction; Haar & Donchin, 2020). This theory was presented in light of the realization that motor imagery performance can result in self-reported errors (Dahm & Rieger, 2019b; T. G. J. Ingram et al., 2022). These errors arise from the comparison of the predicted effects of movement against the intended effect of movement (Figure 2.1B; Dahm & Rieger, 2019b). While the mechanism that results in a predicted error from motor imagery is not well understood, it is hypothesized to be the result of forward modeling during motor imagery performance (Kilteni et al., 2018). However, this hypothesis would not explain how the predicted effects of movement could contain an error. In overt execution, the prediction of movement generated by the forward model is compared against sensory afference from movement using a process called state estimation to recognize errors such that they can be corrected (Todorov & Jordan, 2002). This process of state estimation has typically been associated with the function of the parietal lobe (Haar & Donchin, 2020; Shadmehr & Krakauer, 2008; Wolpert & Ghahramani, 2000). Since movement is not performed in motor imagery, there is no sensory input permitting errors to be recognized and, as such, in Chapter 2 we hypothesized that the overt effects of movement



would be simulated in place of overt execution. The simulated observed effects of movement would provide a measure to allow for state estimation to occur and for errors to be recognized, explaining how participants performing motor imagery could recognize deviations from the expected performance. Furthermore, we believed this function to be tied to the L\_IPL based on the parsimony driven assumption that the region would be performing an analogous function in both motor imagery and overt execution. This chapter produced a null result precluding the ability to assign the L\_IPL responsibility for generating simulated feedback in motor imagery and playing a role in an error detection and correction mechanism.

However, given the importance of the L\_IPL to motor imagery noted in other empirical studies, meta-analyses, and the results from Chapter 4 of this thesis, it is unlikely that the region has no ascribed function in imagery of the complex movement execution task (Hardwick et al., 2018; Héту et al., 2013; S. N. Kraeutner, Keeler, et al., 2016). Therefore, the most plausible interpretations of the null result from chapter 2 remain 1) the L\_IPL is performing a function other than that hypothesized, or 2) the timing of the stimulation did not align with the timing of the hypothesized process for generating simulated feedback, the function ascribed to the L\_IPL. Should the region not be involved in the process of simulating the observed effects of movement, another potential candidate region that could be involved in this mechanism is the cerebellum, as it is thought to be responsible for online control of movement (Miall, 2003; Popa & Ebner, 2019; Shadmehr et al., 2010; Shadmehr & Krakauer, 2008). In this scenario, the cerebellum would be receiving a state estimation from another source in the cortex or would be performing that function in addition to the forward modelling process. The second interpretation of the null result from chapter 2 could suggest that the L\_IPL is not involved in a

comparative function after the cessation of a trial, and rather could only be active during motor imagery performance. The timing of the inhibitory stimulation in chapter 2 was 100ms after the cessation of each trial; this timing was selected to attempt interruption of the comparison of the simulated observed effects of movement (generated by the L\_IPL) against the intended effects. To investigate if the issue was related to timing of the inhibitory stimulation, a follow-up study was pursued in which the timing of stimulation to the L\_IPL was altered, including two groups that received stimulation during motor imagery performance (25% and 50% of the duration of the stimulus animation). Data collection as of July 2023 is nearly complete, and we expect the results to speak to the involvement of the L\_IPL more definitively in the simulation of the observed effects of movement. Should the null hypothesis be rejected in this study, the findings would highlight another potential congruency between motor imagery and overt execution whereby the role of the L\_IPL could be the same in both modalities. In overt execution the parietal lobes are believed to play a function in state estimation which is an essential comparison for online motor control (Haar & Donchin, 2020; Shadmehr & Krakauer, 2008). By demonstrating impaired learning after single pulse TMS delivered to the L\_IPL during motor imagery performance, a more specific role for the area could be elucidated aligning the function of the region in the provision of sensory prediction errors (Figure 2.1C; Solomon et al., 2022). The only difference between the two modalities is that in overt execution sensory information regarding movement is available as the movement is actually performed, whereas that same sensory information would need to be simulated in motor imagery.

#### 5.4 *Theories of motor imagery*

Based on the evidence generated in Chapters 2 and 4 of this thesis, it appears that the L\_IPL is vital for motor learning to occur via motor imagery and further that this region is active during motor imagery performance. While the studies herein cannot define an exact role for the L\_IPL in motor imagery, the area has noted involvement in several components of controlling movement including sensorimotor integration, state estimation, high-order sensorimotor information integration and conscious motor intentions (Buneo & Andersen, 2006; Desmurget & Sirigu, 2012; Fogassi & Luppino, 2005; Shadmehr & Krakauer, 2008; Wolpert & Ghahramani, 2000). If one accepts the parsimonious argument that this region is performing analogous or similar functions in both overt execution and motor imagery, then the parietal lobes should be involved in all stages of motor control from goal and action selection to action execution. The role of the parietal lobes in sensorimotor integration in action selection and execution align well with the motor cognitive model and the perceptual cognitive model, both of which suggest that imagery does not engage the motor system and might serve to explain the increased emphasis placed on the L\_IPL during motor imagery in comparison to overt execution (see Chapter 4; Glover & Baran, 2017; Hardwick et al., 2018; T. Kim et al., 2017; S. N. Kraeutner, Keeler, et al., 2016). Extending this understanding to learning would further imply that behavioural improvements that result from training reflects improvements to the control policy that governs movement, formed in action selection, which aligns with the decreased turn angle correlation seen in Chapter 4 resulting from inhibition via repetitive TMS. Furthermore, while overt execution of movement is noticeably absent in motor imagery there is a bevy of behavioural studies to suggest that motor imagery engages in the forward modelling process and can

generate a predicted outcome for movement that may contain a self-reported error (Dahm & Rieger, 2019b; T. G. J. Ingram et al., 2022; Kilteni et al., 2018). As outlined in section 2.2 of the Introduction to this thesis, this error can only be recognized if the prediction from a forward model is compared against some sensory afference resulting from movement (McNamee & Wolpert, 2019). This sensory information is integrated with the position of the body to detect error in online movement through the process of state estimation, which is yet another proposed function of the parietal lobes (Haar & Donchin, 2020; Shadmehr & Krakauer, 2008). Since sensory afference is lacking in motor imagery, as posited in Chapter 2, we theorized that this information is being simulated during motor imagery performance (see Chapter 2). Therefore, it is also possible that the involvement of the L\_IPL in motor imagery-based motor learning in Chapter 4 reflects a role for the region in state estimation and would therefore support alternate theories of motor imagery, such as motor emulation theory (Grush, 2004). However, it is important to note that these two camps of motor imagery theories are not exclusive and could be reflective of components that form a hybrid theory for motor imagery. Once such possibility could be the combination of the motor cognitive model and motor emulation theory (Hurst & Boe, 2022). It is in this writer's opinion that this combination of the perceptual cognitive model and motor emulation theory presents the most plausible model for imagery as it encapsulates how imagery could lead to better control policies for movement than overt execution by using forward models and some form of simulated state estimation to generate a reward prediction error that in turn reinforces or punishes the selected movement (Hurst & Boe, 2022; Kilteni et al., 2018; T. Kim et al., 2017). Notably many of these mechanisms align with proposed functions of the parietal lobes and would account for why imagery might

rely so heavily on this area of the cortex (Haar & Donchin, 2020; Hardwick et al., 2018; Shadmehr & Krakauer, 2008).

### 5.5 *The influence of task on cortical networks:*

The second purpose of this thesis was to explore the impact of task selection on our understanding of motor imagery-based motor learning. The results of the study highlight that task selection is indeed affecting the conclusions made from individual studies. Specifically, with regards to the three targeted cortical regions, only results from the L\_IPL replicated findings of the previous literature, noting a negative effect of inhibition on motor imagery-based motor learning (S. N. Kraeutner, Keeler, et al., 2016). Inhibitory stimulation to the M1 and SMA demonstrated a facilitation of task performance after motor imagery training and impairment of performance overt execution training. The results in overt execution mirror the literature after stimulation to the M1 supporting its role in the consolidation of learned motor behaviours (Krakauer et al., 2019; Muellbacher et al., 2002; Richardson et al., 2006). In the SMA, the results did differ from previous literature where inhibitory stimulation impacted learning, but not performance of a learned skill whereas the opposite trend was seen in chapter 4 (Solomon et al., 2021). The results of stimulation to the M1 and SMA in imagery not only contrast against the previous literature but indicate credible findings in the opposite directions of the previous literature that denoted no effects or impaired learning as a result of inhibitory stimulation (S. N. Kraeutner, Ingram, et al., 2017; Pelgrims et al., 2011b; Solomon et al., 2021). These contrasting results are the primary evidence for the effects of task selection on the generalization of the results from a singular paradigm to a motor imagery.

It is unsurprising to consider that different tasks have unique representations at the level of the cortex (Genon, Reid, Langner, et al., 2018; Ito & Murray, 2023). Historically, to determine how task performance is represented in the brain, neuroimaging is used to identify which areas of the brain are active and, subsequently, lesion studies can be used to identify if the activity in a region is important to the behaviour (Friston & Price, 2011). However, the result of this line of investigation has led to multiple functions being associated with the same cortical regions making it near impossible to disentangle what the function of any particular region is (Genon, Reid, Langner, et al., 2018). This point is well demonstrated by the heterogeneity of results seen when stimulating the M1 while engaging in a variety of different tasks including a hand laterality judgement task, SRTT and the complex movement execution task employed in this thesis. In the hand laterality judgement task virtual lesions induced by stimulation impaired performance, whereas a virtual lesion prior to motor imagery training on a SRTT had no effect on performance, and finally, a virtual lesion prior to motor imagery training on a complex movement execution task facilitated performance (see Chapter 4; S. N. Kraeutner, Ingram, et al., 2017; Pelgrims et al., 2011b). The different effect of the virtual lesion to M1 on subsequent task performance arise in light of differing levels of M1 activity noted from neuroimaging studies of each paradigm whereby the M1 is not active during motor imagery performance of simple motor tasks, nor during performance of the hand laterality judgement task, but is active during motor imagery of the complex movement execution paradigm (Hardwick et al., 2018; Héту et al., 2013; T. G. J. Ingram, 2021). The results of stimulation prior to the hand laterality judgement task make less sense in light of the lack of activity in the M1 associated with that task (Héту et al., 2013; Pelgrims et al., 2011b). In contrast, the null effect of stimulation prior to motor

imagery training on the SRTT aligns with the lack of M1 activity associated with motor imagery performance of kinematically simple motor tasks but might also reflect the minimal recruitment of M1 associated with the task (Hardwick et al., 2018; S. N. Kraeutner, Ingram, et al., 2017; Yokoi & Diedrichsen, 2019). Likewise, the facilitation of performance associated with M1 stimulation prior to motor imagery training on the complex movement execution task aligns with noted activity in the sensorimotor regions during imagery performance (T. G. J. Ingram, 2021). However, the lack of consistency across this continuum of results makes it impossible to tell what the role of the M1 is in motor imagery, if it plays a role at all, as the data accrued to date on M1 involvement is dependent on task and may or may not be reflective of a function that sub-serves motor imagery or an additionally recruited cognitive function required to perform the task.

#### *5.6 Limitations and future directions:*

Future investigations of motor imagery should seek to overcome the limitations of the 'stimulation deficit design' where TMS is used to induce a virtual lesion and the effects of the virtual lesion are measured on a single behaviour (Genon, Reid, Langner, et al., 2018). The comparison of the results from chapter 4 to the past literature clearly highlights this limitation. Specifically, results from the M1 and SMA do not align with previous literature, introducing ambiguity pertaining to their role or importance in MI. As such, interpreting the results from this thesis that contrast the previous literature would only serve to provide an increasingly complex function of the targeted brain regions that is likely due the specific demands of the task used rather than a consistent function of the corresponding region in motor imagery. Accordingly, the only result that likely reflects a meaningful feature of motor imagery-based

motor learning is that it relies on the function of the L\_IPL based on consistency of the finding with the past literature (Hardwick et al., 2018; S. N. Kraeutner, Keeler, et al., 2016). Interpreting the other credible results of this thesis, in the M1 and SMA, to identify why divergent results occurred is not a fruitful endeavour as the interpretation would only add to an already muddled list of potential functions performed by each area (Bhattacharjee et al., 2021; Nachev et al., 2008). Rather this body of research can be used as an example of the limitations of the stimulation deficit study design and highlights a much-needed change in methodological approach to tie the function of the brain to behaviour.

To overcome the limitation of the stimulus deficit study design, the variability of the measured behaviours needs to be addressed to permit for more consistent inference regarding modalities for motor learning. Two suggestions to produce more consistent findings are: 1) the interpretation of studies could be restricted to distinct components of the behaviour they measure or 2) multiple tasks can be used to identify consistent trends that represent a generalizable result. In the motor control literature, a number of serial conceptual steps have been identified to represent movement and they have been associated with classes of commonly used motor paradigms (Figure 1.2; Krakauer et al., 2019). However, these relationships between paradigms and the behavioural mechanisms can only be established through years of repeated use and a well-established mechanism for motor control, optimal feedback control, which does not exist in the study of motor imagery (Todorov & Jordan, 2002). As such, the alternative solution of using multiple tasks becomes a more viable alternative to reducing the impact of task selection on the generalization of results to the modality of imagery. These methodological aggregation efforts have already been established in the neuroimaging



literature in several open-source initiatives, BrainMap and Neurosynth, that compile results across published data to permit for hypothesis testing across tasks (Fox & Lancaster, 2002; Laird et al., 2005; Yarkoni et al., 2011). While these databases have existed for years, they permit for the use of more advanced analytical techniques that focus on identifying consistency in the behavioural paradigms that activate a given brain region rather than asking which cortical regions are active in support of a behaviour. In taking this approach, these initiatives produce more consistent findings that are less susceptible to epiphenomenon related to experimental methodology (Genon, Reid, Langner, et al., 2018; Genon, Reid, Li, et al., 2018; Poldrack, 2010). This change in methodological approach could be applied to the study of motor imagery, and studies looking to make a claim about the neural mechanisms underlying the modality should use multiple paradigms to ensure that there is consistency of results across tasks. By doing so, future work would increase the probability that inference made about motor imagery from an individual study's result is indeed reflective of a property of the modality and not a by-product of the task, such as an imagined button presses or drawn shapes on a touch screen.

### *5.7 Conclusion:*

In summation, this thesis highlights an incongruence in the behavioural mechanisms explaining how motor imagery can result in an error (Dahm & Rieger, 2019b; T. G. J. Ingram et al., 2022). Based on findings that indicate that a forward model is used during motor imagery performance, akin to overt execution, we posit that state estimation is likewise being performed in imagery and the function has the same cortical representation, the parietal lobes (Haar & Donchin, 2020; Kilteni et al., 2018). While there was not any evidence generated in support of this hypothesis (see Chapter 2), repetitive TMS of the L\_IPL revealed that the area is important

for motor imagery-based motor learning consistent with findings from past stimulation and neuroimaging evidence (Hardwick et al., 2018; S. N. Kraeutner, Ingram, et al., 2017). This result likely means that the null result in chapter 2 was due to a mismatch between the stimulation timing and the proposed function of the L\_IPL and is being further investigated. However, the lack of reproducibility in the other cortical regions inhibited in Chapter 4, the M1 and SMA, demonstrate clear evidence of task related bias and makes interpretation of the findings challenging in light of previously published results (S. N. Kraeutner, Ingram, et al., 2017; Solomon et al., 2021). As such, future investigations of the neural mechanisms underlying motor imagery would be able to limit the impact of task selection by employing a battery of tasks and investigating for consistent effects across them.

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