

INVESTIGATING THE EFFECT OF TASK NATURE ON CORTICOSPINAL
EXCITABILITY DURING MOTOR IMAGERY

by

Hudson J. Barr

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Abstract

Little research has gone into investigating the role of task used in learning via motor imagery. It is possible that our understanding of imagery might be influenced by the task chosen for its study. To ascertain if previous findings were influenced by the task chosen, participants were recruited to perform imagery of a motoric and perceptual task. In a single 2.5-hour session, participants performed imagery of the two tasks followed by physical execution to obtain a measure of performance improvement. Motor-evoked potentials (MEPs) were elicited using transcranial magnetic stimulation (TMS) and recorded during imagery performance, with MEP amplitude compared between tasks for each participant to determine which task led to increased corticospinal excitability. Results indicated that the motor task led to significantly increased excitability, demonstrating that the task used has a meaningful influence on corticospinal excitability and suggesting that the task used may bias our understanding of how imagery works.

List of Abbreviations Used

cTBS - Continuous Theta Burst Stimulation

EMG – Electromyography

FDI – First Dorsal Interosseus

fMRI – Functional Magnetic Resonance Imaging

IPL - Inferior Parietal Cortex

ISL – Implicit Learning Sequence

KVIQ - Kinesthetic Visual Imagery Questionnaire

LJT – Laterality Judgement Task

M1 – Primary Motor Cortex

MCM – Motor-Cognitive Model

MET – Motor Emulation Theory (Grush, 2004)

MEP – Motor-Evoked Potential

MT – Motor Threshold

MST – Motor Simulation Theory

PCM – Perceptual-Cognitive Model

PET – Positron Emission Tomography

PP – Physical Practice

RT – Reaction Time

RMT – Resting Motor Threshold

SRTT – Serial Reaction Time Task

TMS – Transcranial Magnetic Stimulation

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Chapter 1: Introduction

The ability to learn new motor skills and improve those previously acquired is a crucial aspect of our lives. Motor skill learning refers to the process of executing learned movements more quickly and accurately with practice (Newell, 1991). While physical practice is the most common method for motor learning, motor imagery, the mental rehearsal of a movement (Jeannerod, 1995), has been shown to be effective as well. Motor imagery can be performed in either first or third person perspective, and can focus on either the kinesthetic or visual aspects of the movement (Jeannerod, 1995; Lotze & Halsband, 2006). Evidence shows that kinesthetic imagery is more effective than visual imagery in activating the motor cortex and facilitating motor learning (Mulder, 2007; Ruffino et al., 2017; Stinear et al., 2006)

There are five competing theories on motor imagery, with motor simulation theory having the largest impact. Motor simulation theory proposes that motor imagery is a functionally equivalent covert simulation of actual movement, with similar elements as actual movement but with actual movement inhibited (Jeannerod, 2001, 2004, 2006; O'Shea & Moran, 2017). There is substantial evidence supporting functional equivalence, including peripheral measures of physiological arousal and congruence between the time it takes to complete an imagined or actual movement (Collet et al., 2011; Decety, 1996; Guillot et al., 2007; Guillot & Collet, 2005; O'Shea & Moran, 2017; Papadelis et al., 2007). However, the neuroimaging evidence in support of functional equivalence is mixed, with inconsistent activation of the primary motor cortex during motor imagery compared to actual movement (Héту et al., 2013; O'Shea & Moran, 2017).

There is a gap in the literature pertaining to the role of the task in learning via imagery. If one considers motor tasks as falling somewhere on a perceptual-motor spectrum, then it could be that the tasks used in much of the research examining motor imagery, namely stimulus response time tasks that tend to emphasize perceptual rather than motor components of movement, are producing evidence biased toward the mechanisms of motor imagery being more perceptual. Therefore, the objective of the current study is to gain a better understanding of the mechanisms underlying motor imagery, specifically the influence of task nature on corticospinal excitability when performed via imagery . The study measured corticospinal excitability during imagined performance of two tasks – one more perceptual and one more motoric - to explore how task nature affects corticospinal excitability during imagery. The hypothesis is that the amplitude of motor-evoked potentials obtained via transcranial magnetic stimulation will be higher for the motor task compared to the perceptual task. The results of this study support the hypothesis that motor-evoked potentials obtained through transcranial magnetic stimulation have a higher amplitude for the motor task than the perceptual task. These findings suggest that the choice of task can influence conclusions about the mechanisms of motor imagery, serving as a cautionary note for future researchers but also highlighting an uncharted and promising direction in the field.

Chapter 2: Literature Review

2.1 Motor Learning

From shortly after we are born and until the day we die, learning new motor skills and improving those previously acquired plays a salient and fundamental role in our daily lives. Motor skill learning refers to the process that learned movements are executed more quickly and accurately with practice (Newell, 1991). In general, the initial learning of these skills is relatively fast (such that improvements can be seen within a single training session) and then slow down, with further gains developing incrementally over many practice sessions. However, what can be defined as fast and slow learning is highly task specific. For example, the fast-learning stage of learning a four sequence key-press could last minutes, whereas the fast stage of learning to play a piece of music could take months (Dayan & Cohen, 2011).

Though it may not account for all observed variance, the positive relationship between time spent practicing a motor skill and level of performance is prevalent throughout the literature (Macnamara et al., 2016). Take for instance a series of studies that looked at the average hours of practice between musicians of different skill levels. Across all musicians and musical instruments in the study, group averages of time spent practicing were higher for the most accomplished musicians and lower for the least accomplished musicians (Ericsson et al., 1993). This relationship between practice and outcome can similarly be seen in recovery of motor function following a stroke. For instance, a meta-analysis by Lohse et al (2014) (Lohse et al., 2014) showed a positive relationship between the time scheduled for therapy and improvement of outcome. This relationship is echoed in a more recent clinical trial which showed that intensive upper

limb rehabilitation in chronic stroke patients led to clinically important improvements in their recovery (Ward et al., 2019) , even after the early post-stroke phase often considered the optimal window for treatment to occur (Krakauer et al., 2012).

At its most fundamental level, motor learning creates changes in the way that the cells of the brain, called neurons, communicate with each other (Papale & Hooks, 2018). Neurons communicate with each other by means of electrochemical signals at the junctions between adjacent neurons, or synapses. At the synapse, neurotransmitters are released from the axon terminal end of the pre-synaptic neuron, and then act on the dendrite of a post-synaptic neuron, which can then cause the post-synaptic neuron to send its own electrochemical signal to another neuron. All synapses are capable of being modulated through activity-dependent changes in synaptic strength, say through the repetitive nature of practicing a musical piece or slapshot (Bruel-Jungerman et al., 2007; Gillick & Zirpel, 2012). As demonstrated in early animal research (Nudo et al., 1996; Plautz et al., 2000), motor learning occurs from the repetitive practice of motor skills, when after enough practice, changes in the structure and function of our brains are made through a process called neuroplasticity (Dayan & Cohen, 2011). The method or modality used to practice a motor skill and make these long-term changes can differ. The most familiar method of motor learning, physical practice (PP), is also the most effective. However, other methods of motor learning have also been shown to be effective, with one of such methods being motor imagery.

2.2 Motor Imagery

Motor imagery refers to the imagined rehearsal of a movement (Jeannerod, 1995). While practicing a movement through repetitive PP, also called physical execution, is

recognized as the primary approach to motor learning, motor imagery has consistently demonstrated a similar ability to facilitate motor learning across numerous disciplines (Driskell et al., 1994). Evidence for which comes from previous research that showed PP led to improved motor performance compared to motor imagery, but practice using motor imagery led to improved motor performance compared to no practice (Gentili et al., 2006). This has led to interest in motor imagery research for the purposes of learning in circumstances where PP is not an option, such is the case for rehabilitation following a brain injury (Lotze & Halsband, 2006; Page et al., 2001).

Motor imagery can be performed from two different perspectives (Jeannerod, 1995): the first person and the third person, where performing motor imagery in the first-person perspective is like looking out of the eyes of the imager while performing motor imagery in the third person perspective constitutes visualizing the movement from an outside perspective (Lotze & Halsband, 2006). In addition to these different perspectives, motor imagery can focus on two different sensory aspects of the movement: kinesthetic and visual. In kinesthetic motor imagery, the focus is on the mechanical and tactile sensations of the movements while visual motor imagery focuses on imagining how the movement looks (Lotze & Halsband, 2006). For the purposes of acquiring basic motor skills, it has been demonstrated that kinesthetic motor imagery is more effective than visual motor imagery as it activates the motor cortex to a greater extent than visual imagery, thus it is used more often in motor imagery research paradigms (Mulder, 2007; Ruffino et al., 2017; Stinear et al., 2006).

Although the field of motor imagery research continues to grow, the mechanisms of motor imagery remain unclear and have led to the creation of five competing theories:

motor simulation theory (MST) (Jeannerod, 2001), motor emulation theory (MET) (Grush, 2004), the motor-cognitive model (MCM) (Glover & Baran, 2017), the perceptual-cognitive model (Frank & Schack, 2017), and the effects imagery model (Bach et al., 2021) (see Hurst & Boe, 2022 for a review) (Hurst & Boe, 2022). Of the theories, MST has had the largest impact as it was the first to propose explanations for how cognitive states like motor imagery, action intention (the translation of a desired movement into behaviour), and action-observation, are related to actual motor execution states (Jeannerod, 1994, 1995, 2001). The central tenant of MST is that these motor cognitive states activate similar motor systems to those activated during motor execution, with the proposed reason being that both states share the same motor representations in the mind (Jeannerod, 1994, 2001; O'Shea & Moran, 2017). More specifically, MST proposes that motor imagery is a functionally equivalent covert simulation of actual movement that contains the same elements as an actual movement except that actual movement is inhibited (Jeannerod, 2001, 2004, 2006; O'Shea & Moran, 2017).

In a recent review of the theories and models of motor imagery, Hurst and Boe (2022) discuss how each theory relates to the notion of functional equivalence proposed in MST, categorizing the different theories of motor imagery based on the extent to which they agree with functional equivalence. The rationale being that for theories more closely aligning with functional equivalence (i.e., MST and MET), imagery and action are thought to use the same neural pathways up to the point of execution. This contrasts with motor imagery models that propose a divergence from functional equivalence (i.e., MCM and PCM) which argue imagery requires pathways and cognitive systems beyond those used during action. There is a substantial body of evidence in support of motor

imagery being a functionally equivalent covert counterpart to actual movement (O'Shea & Moran, 2017). For instance, peripheral measures of physiological arousal like skin resistance, heart rate and electromyography (EMG) activity have been shown to correlate between imagined and actual movement (Collet et al., 2011; Guillot et al., 2007; Guillot & Collet, 2005; O'Shea & Moran, 2017; Papadelis et al., 2007). Since these physiological measures are largely outside of voluntary control, the similarity in activation between movement and imagery suggest that both movement types have a central origin (O'Shea & Moran, 2017). This is further evidenced by the congruence between the time it takes to complete an imagined or actual movement (i.e., mental chronometry), and imagined movements are consistently shown to account for motor rules like Fitts Law, the speed-accuracy trade off of movement (Decety & Jeannerod, 1996).

However, the neuroimaging evidence in support of functional equivalence is mixed. While composites of data gathered from neuroimaging studies of motor imagery highlight a significant overlap of shared brain regions between imagined and actual movement (Hétu et al., 2013; O'Shea & Moran, 2017), the primary motor cortex (M1) (a brain region implicated in motor skill learning and movement (Classen et al., 1998; Pascual-Leone et al., 1995; Tallent et al., 2021)), is inconsistently activated during motor imagery compared to actual movement (Hardwick et al., 2018; Hétu et al., 2013) (Figure 1). Conversely, the evidence in support of functional equivalence deriving from studies using transcranial magnetic stimulation (TMS) (discussed in further detail below) seem to implicate the involvement and activation of M1 during imagery (see studies by Stinear et al., 2006 & Yoxon and Welsh, 2019 for examples) (Stinear et al., 2006; Yoxon & Welsh, 2019). Evidence for M1's involvement during motor imagery from TMS studies does not

go uncontested as other studies have shown that inhibition of M1 via a type of TMS called continuous theta burst stimulation (cTBS) does not impair motor imagery performance (S. N. Kraeutner, Ingram, et al., 2017). It is important to acknowledge some of the limitations regarding the use of cTBS. For instance, previous literature has shown variability in the inhibitory effects of cTBS experienced by participants, with some participants being unresponsive to the stimulation with little to no evidence of an inhibitory effect (Hamada et al., 2013). Despite the variability in the inhibitory effects of cTBS, more recent reviews demonstrate its net effect to be inhibitory (Chung et al., 2016; Wischnewski & Schutter, 2015). Moreover, by using the same cTBS protocol and experimental task, Kraeutner et al. (2016) showed that inhibition of the inferior parietal lobe (IPL), a brain region implicated in the encoding of perceptual information to movement goals (Bapi et al., 2006; Cooke et al., 2003), impaired motor imagery-based learning (S. N. Kraeutner, Keeler, et al., 2016) – an effect echoed in lesion-based studies investigating the impacts of parietal damage on motor imagery performance (McInnes et al., 2016; Oostra et al., 2016). Taken together, it is therefore likely that the overall effect of cTBS is inhibitory. And, given that the activation and involvement of M1 is the kingpin for theories that more closely align with functional equivalence, the fact that learning via motor imagery can occur despite the inhibition of M1, but could not with inhibition of IPL, suggests that learning via motor imagery is not simply the covert counterpart to PP and may be more perceptual in nature.

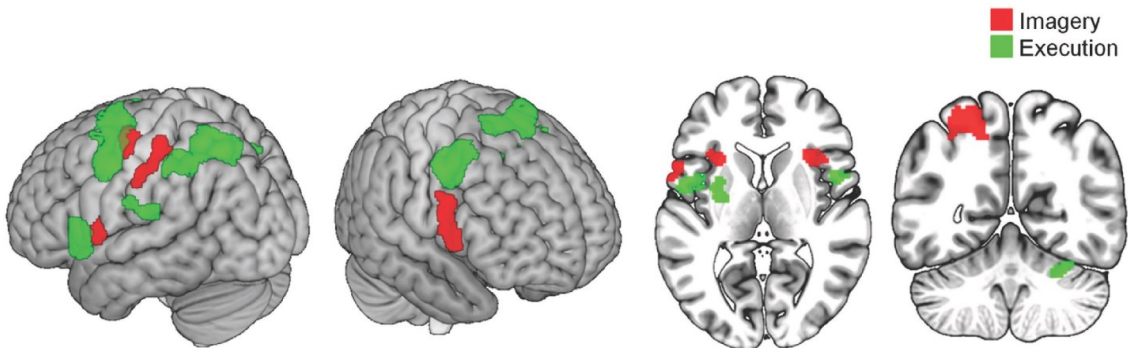


Figure 1. Contrast Analysis of Brain Activity shared between Motor Imagery and Execution. Contrast analyses of brain regions involved in motor imagery (red) and ME (green), highlighting a lack of overlap in M1 between the two learning modalities (adapted from Figure 3 in Hardwick et al., 2018).

While the study by Kraeutner et al. (2017) suggests learning still occurs via motor imagery despite inhibition of M1, it is important to consider whether the results could have been influenced by the type of task selected. It may be that previous studies investigating the neural underpinnings of motor imagery have biased findings that emphasize more perceptual learning vs. motor learning. For example, the task used in the TMS study by Kraeutner et al. (2017) was an implicit sequence learning task (ISL; described in more detail below) in which the participants had to imagine pressing the corresponding key on a keyboard in response to an auditory cue. It could be that this task, rather than the mechanisms underpinning motor imagery, is more perceptual in nature and would not preferentially activate the motor system to the same degree as a more ‘motoric’

task would. Therefore, learning could still occur despite inhibition of M1 because the task is biased to perceptual learning, rather than motor imagery being only perceptual in nature (Figure 2). Viewed through this lens, it is possible to categorize the theories of motor imagery on another spectrum: the perceptual-motor spectrum, with one end of the spectrum being more perceptual (PCM, MCM) and the other more ‘motoric’ (MST, MET). Therefore, there is a need to study different outcomes (like corticospinal excitability) to better understand the nature of what motor imagery might be doing.

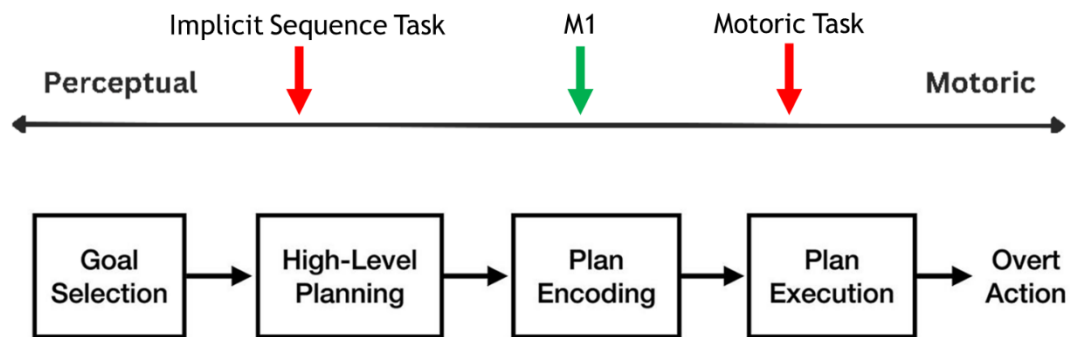


Figure 2. The Perceptual-Motor Spectrum. Illustrates what a perceptual-motor spectrum may look like by highlighting that an implicit sequence task (red) may preferentially activate brain regions corresponding to different stages of motor execution than a motor task (red), which may in-part explain the inconsistent activation of M1 throughout the literature.

2.3 Corticospinal Excitability

As previously mentioned, motor learning is thought to occur via a property of the brain called plasticity (Dayan & Cohen, 2011). This plastic property allows for functional and structural changes to be made to cortical representations and neural networks in response to our ever-changing internal and external environments (Buonomano & Merzenich, 1998; Ruffino et al., 2017). Without this property, motor learning, and learning more generally, would not be possible. However, the level of plasticity in the brain is equally as important where having too much or too little would provide the same result preventing long-term learning. Therefore, mechanisms in the brain must strike a balance between high and low plasticity through excitatory and inhibitory mechanisms (Abbott & Nelson, 2000).

Corticospinal excitability is a measure of brain excitability and refers specifically to the efficacy of corticospinal pathways to relay neural signals from the central nervous system to the locomotor muscles (Vøllestad, 1997; Weavil & Amann, 2018). Through the use of TMS, corticospinal excitability can be quantified as a motor-evoked potential (MEP) when measured using EMG (Figure 3) (Cirillo et al., 2011; Hallett, 2000). Through delivering a brief magnetic pulse over a participant's cortex, an MEP can be produced, the magnitude of which can be altered based on several factors including the intensity of stimulation and the excitability of the neuronal cell membrane (Hallett, 2000). Ziemann (2004) demonstrated that because the threshold for producing an MEP can be altered when drugs that affect sodium and calcium channels, that it must also indicate membrane, and thus corticospinal excitability (described in detail in the section below) (Ziemann, 2004).

Currently, it is generally accepted that an increased level of corticospinal excitability is a pre-requisite for any experience-dependent changes in plasticity, and thus motor learning, to occur (Avanzino et al., 2015). Put another way, corticospinal excitability is increased when the neurons in the cortex and spinal cord are in an excited state, meaning their resting membrane potentials are closer to the threshold for depolarization. Therefore, the increased excitability in the neurons require less stimulus to trigger an action potential, and thus makes any experience-dependent changes in the neural connections more likely to occur (Lee et al., 2021).

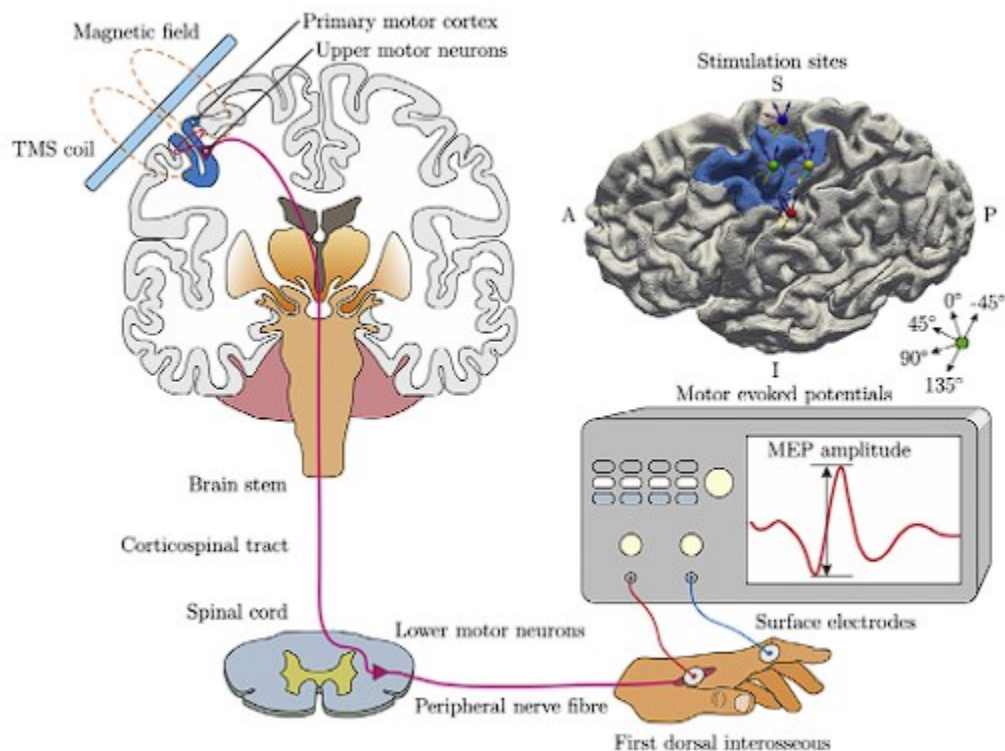


Figure 3. Schematic representation of application of TMS and Measurement of MEPs. A schematic depicting the neurophysiological response to TMS. Electrical current running through the coil generates a magnetic field which in turn generates a second electrical current that passes through the skull etc. and depolarizes neurons that give rise to the corticospinal tract, resulting in a response in the target muscle that can be quantified as an MEP when surface electrodes are placed over the target muscles (Weise et al., 2020).

2.4 Transcranial Magnetic Stimulation

Neuroimaging techniques like positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) have consistently demonstrated similarities in activated brain regions between motor imagery and execution. However, they cannot prove that any given brain regions are shared between the two learning modalities as fMRI and PET are both indirect measures of cortical activity in that both depend on cerebral blood flow. For example, fMRI uses the BOLD response to conclude that an area is ‘active’ because of increased flow of oxygenated blood to the region during a task. Forms of non-invasive brain stimulation such as TMS do not depend on such a response, and rather reflects the excitability of the neurons directly. This is evidenced in an activation likelihood estimate analysis by Héту et al. (2013) where a total of 75 motor imagery papers using neuroimaging were quantitatively summarized for the purpose of providing a comprehensive map of brain structure involved in motor imagery. In the analysis, the authors make note that there are certain brain regions, like M1, that have inconsistent results depending on the study. However, when alternative instruments are used such as those that can deliver non-invasive forms of brain stimulation, results of M1 activation become more consistent (Héту et al., 2013). As such instruments that can deliver non-invasive forms of brain stimulation have become popular in the fields of motor imagery.

Of the different types of non-invasive brain stimulation, TMS has become the most widely used due largely to its ability to target a robust array of brain regions and it causing less discomfort than its cousin, transcranial electrical stimulation (Hallett, 2000). Compared to neuroimaging techniques like fMRI and PET, TMS offers the advantage of

having high temporal resolution and can be used to create temporary functional lesions through inhibiting a region of the brain by generating a powerful magnetic field (Bolognini & Ro, 2010). This is achieved using two key physics principles: the Biot-Savart Law and Faraday's Law. According to the Biot-Savart Law, an electric current that is ran through a coil of wire will generate a magnetic field perpendicular to the plane of the wire. Faraday's Law states that a magnetic field generated by a current will produce its own electric field perpendicular to that magnetic field. It is this final electric field that has a primary effect on the brain's transmembrane potential when using TMS (Figure 4) (Walsh et al., 2003).

Ions flow in the brain in response to the electric field produced by TMS, altering the balance of electric charge stored on either side of the cell's membrane and depolarizing or hyperpolarizing the cells in the process (Rossi et al., 2009). When stimulation is delivered over a participant's M1, it induces descending volleys in the pyramidal tract that projects to spinal motoneurons. Each TMS-induced descending volley causes the release of the excitatory neurotransmitter glutamate, depolarizing the spinal motoneurons. When the spinal motoneuron is sufficiently excited by glutamate, it triggers an action potential that propagates down a peripheral motor axon towards the skeletal muscle which elicits a motor response (Farzan, 2014). The specific skeletal muscle which elicits a response depends on where TMS was delivered over M1 as skeletal muscles have cortical representations in M1, and this motor response can be measured as a MEP when electrodes are placed over the skin above the target muscle and recorded using EMG (Cirillo et al., 2011; Hallett, 2000; Klomjai et al., 2015).

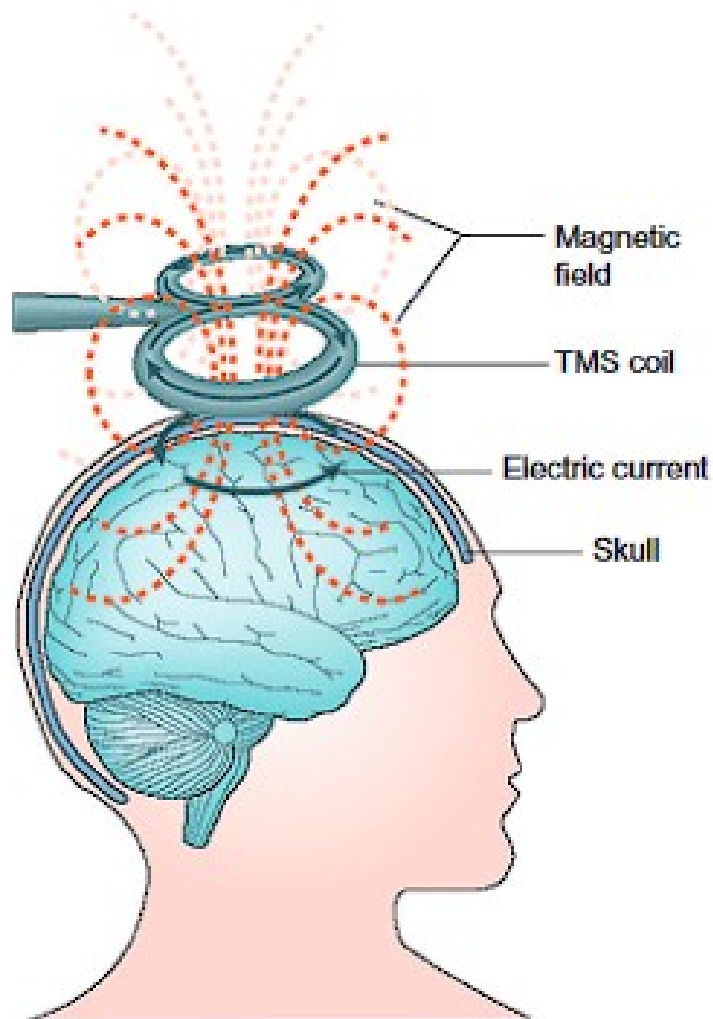


Figure 4. The Physical Mechanisms of TMS. An artists depiction of the electrical current induced in the brain through the magnetic field (dashed lines) produced by magnetic pulses applied via a figure-eight-shaped coil positioned above the scalp (Spronk et al., 2011).

Single pulse TMS

The application of stimulation in TMS can vary based on the intended result. There are three main types of TMS: single pulse, paired pulse, and repetitive stimulation. In paired pulse stimulation, two stimuli are delivered in close succession, while repetitive TMS

involves the rapid delivery of multiple stimuli. The present study focuses on single pulse TMS (for more information on other forms of TMS, see Rossini et al., 2015). Single pulse TMS has high spatial and temporal resolution (Bolognini & Ro, 2010; Hallett, 2007) and involves administering a single stimulus, which is typically delivered at the threshold or suprathreshold level (Rossini et al., 2015). To ensure that the observed effects are solely due to the stimulation, the interstimulus interval must be at least 3 seconds to allow corticospinal neurons to return to their resting state between stimuli (Rossini et al., 2015).

Motor Threshold

Using the MEP recorded from TMS as a proxy for corticospinal excitability has propelled motor imagery research in recent years. This is in large part due to the magnitude of a participant's MEP changing without any significant changes to the participant's motor threshold (MT); a measure which represents an individual's level of excitability and integrity in their corticospinal pathways (Farzan, 2014). Motor threshold can be identified with the target muscle at rest and is aptly named the resting motor threshold (RMT), or during the active voluntary contraction of a target muscle, referred to as active motor threshold. The present study uses RMT; readers are referred elsewhere for more information regarding active motor threshold (see Farzan, 2014). Resting motor threshold is often defined as the minimum stimulation intensity at which the target muscle produces an MEP with a peak-to-peak amplitude of $\geq 50 \mu\text{V}$ in at least 50 % of trials when ten consecutive single pulses are applied with the TMS coil fixed on the hot spot of the target muscle (Farzan, 2014; Rossini et al., 1994). While RMT cannot be directly compared between individuals, each participant's MT can be used as a baseline to which changes in the magnitude of their MEPs can be compared (Ziemann, 2004). Meaning, for

instance, that if the amplitude of a participant's MEPs increase either during or following the performance of a task using motor imagery when compared to the amplitude at the same stimulator output while at rest, then it can be reasoned that motor imagery influenced this change, a finding consistently demonstrated throughout the literature (Munzert & Zentgraf, 2009). For instance, a study by Kasai et al. (1997) investigating the impact of motor imagery on specific groups of motoneurons found that internal motor commands generated by motor imagery can increase cortical excitability without any change in the excitability of the motor neuron pool at the spinal level, as indicated by an increase in the amplitude of the MEP of the flexor carpi radialis muscle with no change in the amplitude of the H-reflex (Kasai et al., 1997). The absence of modification at the spinal level implies that changes influence excitability (evidenced by the increase in MEP amplitude) is confined to the cortical structures and pathways that give rise to the corticospinal tracts. Moreover, this finding indicates that motor imagery is playing a role in the observed changes in MEP amplitudes. In addition, a study by Sohn et al. (2003) expanded what was known about the modulatory effects motor imagery could have on MEPs and demonstrated that motor imagery could lead to a *reduction* in MEP amplitude. In this study, participants were instructed to imagine suppressing TMS-induced twitching movements of their hands by relaxing more after hearing an auditory cue. The authors found that this technique resulted in a significant reduction in MEP amplitude (Sohn et al., 2003).

In summary, TMS has been instrumental in advancing recent research in the field of motor imagery. TMS offers several advantages over neuroimaging techniques, including but not limited to superior temporal resolution and cost-effectiveness. The unique properties of TMS and the MEP it evokes have provided valuable insights into the nature of motor

imagery and its role in the corticospinal pathways. By using TMS, researchers have been able to investigate corticospinal excitability during motor imagery, action execution, and motor execution (Roosink & Zijdwind, 2010). Overall, the use of TMS has greatly contributed to our understanding of motor imagery and its neural mechanisms, but there is still much to learn regarding the nature of motor imagery such what role the motor task has.

2.5 Task Type

The efficacy of motor imagery as a modality for motor learning is influenced by the task's properties, and few studies compare the influence of different imagined task types on motor learning outcomes when using imagery (Ladda et al., 2021). Much like memory, motor imagery tasks can be categorized as either explicit and implicit tasks (Hétu et al., 2013). Explicit imagery involves the deliberate imagination of a particular movement, like imagining how it feels to throw a basketball. Conversely, implicit imagery usually refers to imagery of task-related actions being induced subconsciously when participants are asked to complete a particular task, with one such example of this being the hand laterality judgement task (LJT) (Parsons, 1994). In the LJT, participants are asked to report the laterality (i.e., whether the body part is “left” or “right” with respect to a first-person view) of body parts displayed at various angles and degree of rotation. The LJT is believed to implicitly trigger motor imagery as individuals typically mentally rotate their own limbs to determine the orientation of the body part displayed (Parsons, 2001). Therefore, the LJT can be considered implicit motor imagery as participants are given no instruction on how to complete the task (Parsons et al., 1995). While implicit motor imagery tasks may be used effectively when participants lack experience using imagery (Ladda et al., 2021), explicit motor imagery tasks remain the

most commonly used as using imagery for the purposes of motor skill acquisition requires deliberate, or explicit, practice.

Prevalent throughout the literature examining the acquisition of motor skills via both physical execution and motor imagery are tasks that require the participant to respond to a stimulus using their finger (or in some instance foot). As the finger is frequently used, these tasks are often referred to broadly as ‘finger tapping’ tasks. In its most basic form, a finger tapping task is a motor sequence learning task which involves the use of the fingers to tap out individual elements of a sequence in which they are a part (Figure 5) by using either the keys on a keyboard or another form of response box (Cellini, 2017). The type of finger tapping task used can differ and depends on the given research question. In instances where the researchers are interested in assessing something related to movement, the task acts merely as a paradigm to elicit movement (albeit with a measurable outcome to ensure adherence and uniformity across participants). For example, numerous studies have used finger tapping tasks to assess movement-related brain activity (Karni et al., 1995), and more recently to assess the same in motor imagery (S. Kraeutner et al., 2014). Sequence learning tasks (a form of finger tapping task) have been used extensively to study processes critical to learning and memory (Schwarb & Schumacher, 2012), the most common being the serial reaction time task (SRTT) in which participants are instructed to respond to elements in a sequence as accurately and quickly as possible.

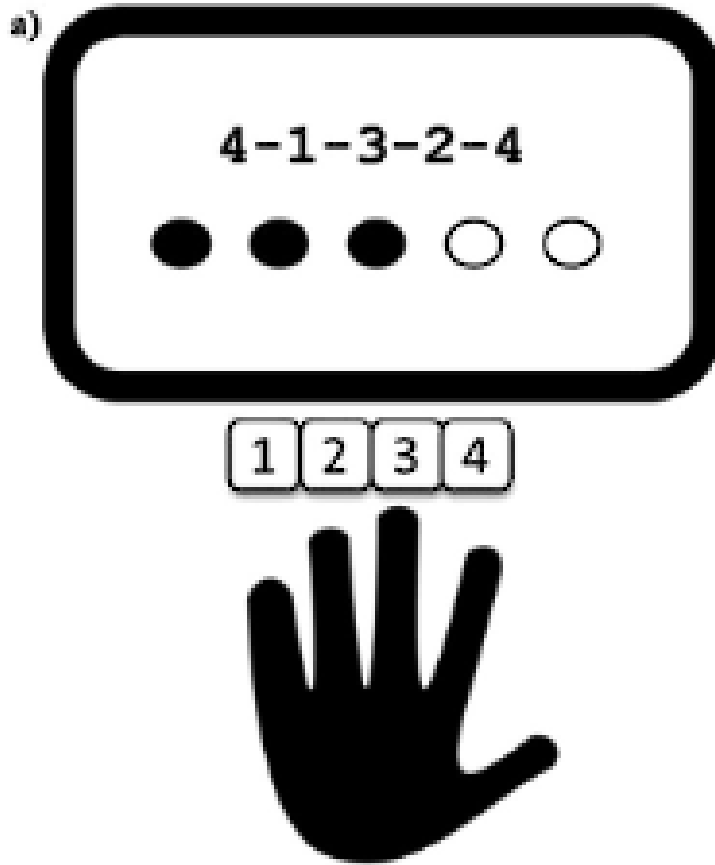


Figure 5. The Fundamental Components of a Finger Tapping Task. The participant's index, middle, ring, and pinky fingers are assigned to specific keys on a keyboard. The participant listens for a cue and responds by pressing the corresponding key. In this example, the index, middle, ring, and pinky fingers of the participant's left hand are mapped to keys 4, 3, 2, and 1, respectively. Therefore, upon hearing the cue sequence "4, 1, 3, 2, and 4", the participant would tap the keys in the following order: 4 with their index finger, 1 with their pinky finger, 3 with their middle finger, 2 with their ring finger, and 4 with their index finger to complete the sequence (Cellini, 2017).

2.5.1 Perceptual Task

Motor imagery studies using variations of the SRTT or other 'finger tapping tasks' have raised some controversy in the field of motor imagery, namely in regard for possible differences in the way these paradigms are learned when practiced using imagery or PP. Such paradigms require participants to associate a perceptual cue (the

stimulus) with a corresponding motor response, such as tapping or imagining tapping a key using the corresponding finger in response to an auditory cued number (e.g., spoken word '1' corresponds to using the index finger to press a key). Motor imagery research has shown performance gains in these tasks using motor imagery practice, the magnitude of which matches that achieved using PP (S. N. Krautner, MacKenzie, et al., 2016). As the nature of the task used (SRTT like sequence learning) raised questions about the type of learning that occurred (i.e., perceptual vs. motor), subsequent work sought to distinguish imagery-based learning from that occurring via PP in the task. To investigate this, Ingram et al. (2016) used the same ISL task, in which participants repeat seemingly random sequences (in response to a cue) that in actuality contain an embedded sequence that repeats (Goschke & Bolte, 2012; Nissen & Bullemer, 1987). As above, prior research established the ISL as suitable for studying motor imagery-based skill acquisition, whereby reaction time (RT) decreased for the repeated but not random sequence elements (Figure 6A)(S. N. Krautner, MacKenzie, et al., 2016). Ingram et al. (2016) randomly assigned participants to perform the ISL task using motor imagery or PP which was then followed by one of two transfer conditions. One transfer condition involved a switch from trained to untrained hand (motor transfer), while the second involved a switch from auditory to visual cues (perceptual transfer). These motor and perceptual transfers permitted assessment of motor and perceptual components of skill acquisition respectively. Data from previous work in which participants performed the ISL via motor imagery or PP but did not undergo a transfer condition was used as a control group.

Task learning was measured by the effect size of the difference in RT between repeated and random sequences, where a larger effect size indicated a greater difference

in RT between the sequences. The results of the study indicated that transfer conditions significantly reduced learning compared to the control group (Figure 6B). In the motor imagery-based training group, perceptual transfer had a greater negative impact on performance compared to the PP-based training groups. Interestingly, motor transfer equally disrupted both the motor imagery- and PP-based training, which the authors attributed to motor imagery-based training relying on both perceptual and motor learning, while PP-based training relies more on motor learning. The authors also noted that motor imagery-based training is likely to rely more on perceptual learning, as it lacks the sensory feedback present in PP-based training. This notion is supported by previous neuroimaging studies that showed increased parietal lobe activity when performing motor imagery (Héту et al., 2013), a brain region involved in the processing of perceptual information (Fogassi & Luppino, 2005; Wise et al., 1997). Furthermore, studies have shown that damage or inhibition of this region impairs motor imagery-based practice effects (S. N. Kraeutner, Keeler, et al., 2016).

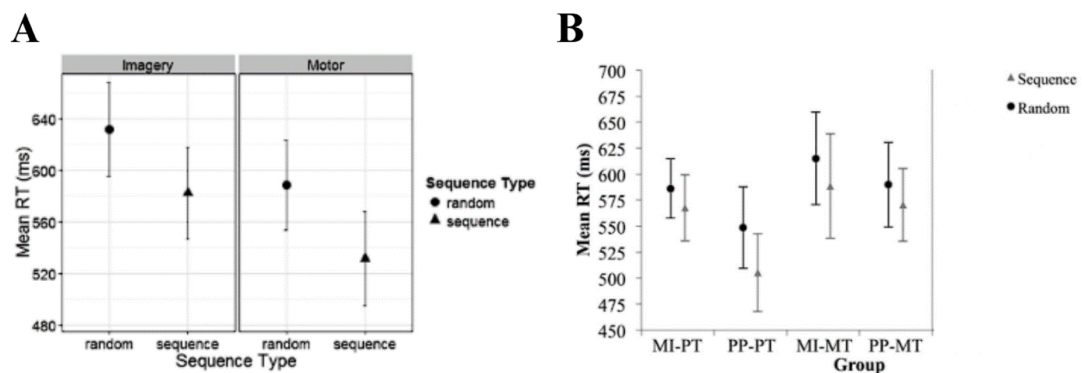


Figure 6. Effects of Sequence Type, Modality, and Perceptual Transfer on SRTT Performance. (A) Group averaged RTs across sequence type demonstrating skill acquisition through imagery in a novel task evidenced through decreased RTs for the repeated but not random sequence elements in both imagery and physical (motor)

practice (S. N. Kraeutner, MacKenzie, et al., 2016). (B) Group averaged RTs for random (black circles) versus implicit (gray triangles) sequences demonstrating the effect of transfer condition and modality of learning on RT (*Ingram et al., 2016; S. N. Kraeutner, Ingram, et al., 2017*).

2.5.2 Motoric Task

In a later study, Ingram et al. (2019) further investigated the nature of motor imagery-based learning using a novel motor task, with the rationale for using this task being attributable to aforementioned concerns surrounding tasks similar to the SRTT (Ingram et al., 2019). According to the authors, it is possible to achieve performance gains through perceptual mechanisms, like the improved recognition of a target, rather than motor mechanisms like improved execution of a movement (i.e., improving kinematics). Said another way, improved RTs can be observed in absence of any change to a given movement, rather the performance gain is achieved through improved mapping of the perceptual stimuli to the motor response. The authors further reasoned that in tasks akin to the SRTT, how the action (i.e., how the key is pressed) is carried out is of little importance (Wong et al., 2015). In comparison, other tasks require intricate motor plans that include specific kinematic parameters, such as instructing participants to press a key lightly with the index finger but hard with the pinky. The novel task by Ingram and colleagues had participants repeatedly reproduce unfamiliar kinematic trajectories, or shapes, and assessed learning and performance through changes in the speed-accuracy function (SAF) over five sessions. To control for familiarization effects, the task consisted of repeated and random trajectories, with randomly generated trajectories used as a control to assess general task performance. Participants were split into either a PP, motor imagery, or a perceptual control (PC) group, with participants in the PC group only

observing trajectories and reporting on the number of times it changed direction to ensure they attended to the stimulus. Participants in the PP group were further divided into two groups, with one group receiving added visual feedback of task performance and the other receiving no feedback of task performance. Regardless of group designation, all participants physically performed the task in the final session of the experiment. In the results of the final session, participants in the motor imagery group performed better than participants in the PC group as well as the initial session of participants in the PP group (Figure 7). The authors noted the significance of these results was that motor imagery appeared to contribute to motor learning at later stages of processing by developing and improving on a motor plan, even in the absence of sensory feedback: the presence of which is a long-assumed requirement for motor learning (Franklin et al., 2007; Lefumat et al., 2016).

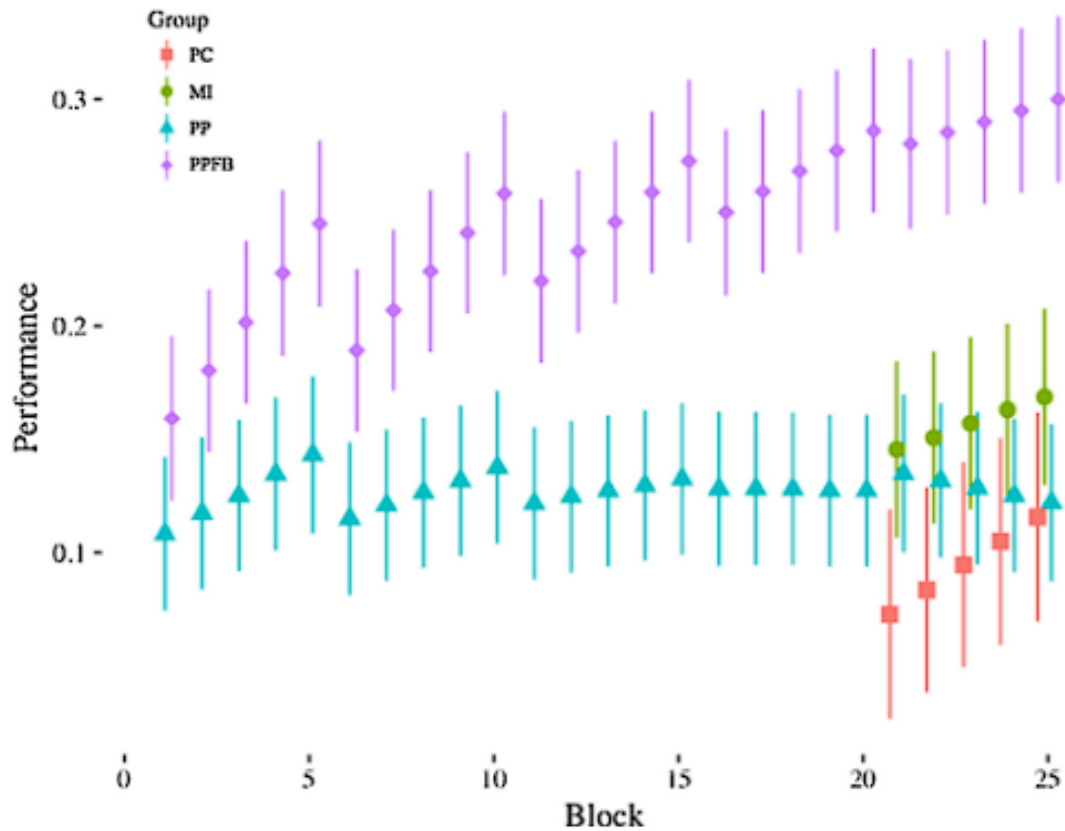


Figure 7. *Effect of Learning Modality on Performance.* Demonstrates learning across the experimental blocks for each group, with learning defined as increased performance over time. There are no estimates in the motor imagery and PC groups as there was no physical performance data collected (Ingram et al., 2019).

2.5.3 Summary

In summary, this literature review highlights the conflicting evidence surrounding the true nature underlying the mechanisms of motor imagery. The review of motor imagery theories and models by Hurst and Boe (2022) shows that there are different theories and models of motor imagery that either agree or disagree with the notion of functional equivalence, and the involvement of M1 in motor imagery remains mixed. While fMRI and PET studies offer little evidence for the involvement of M1 during

motor imagery, studies using TMS suggest that M1 may be involved. Nonetheless, the fact that learning can occur via imagery when M1 is actively inhibited suggests that motor imagery may be its own phenomenon that is more perceptual in nature. The existing body of motor imagery research has investigated different mechanisms of motor learning that may be preferentially used when practiced or learned via motor imagery, but there is a gap in the literature regarding the influence of a task's nature on motor learning via imagery. Therefore, findings from research using tasks of a more perceptual design should be critically evaluated, as any conclusions about the mechanisms underlying motor imagery drawn from such studies may be biased. To elucidate the role of M1 in motor imagery and its underlying mechanisms, future research should directly compare the effect that the type of task, such as perceptual or motor, has on corticospinal excitability. Ultimately, a better understanding of the underlying mechanisms of motor imagery will have implications for the development of new approaches to motor rehabilitation and skill acquisition.

Chapter 3: Objectives & Hypothesis

The above sections have presented an argument that current evidence does not adequately account for the effect that task nature has in motor imagery. Thinking of motor tasks on a perceptual-motor spectrum offers a novel avenue for motor imagery researchers to explore, and exploring how task nature affects corticospinal excitability during imagery may provide insight into the mechanisms involved in imagery as well as the role of M1. Furthermore, understanding the role of task nature in imagery practice could be crucial in prescribing motor imagery as a therapeutic treatment or learning aid for skill acquisition.

The overarching aim and primary objective of this thesis was to gain a better understanding of the mechanisms underlying motor imagery, specifically the role of M1 in motor imagery and the influence of task nature on motor learning via imagery. To achieve this aim, the study measured corticospinal excitability during imagined performance of two motor tasks. Participants were not exposed to the task prior to the experimental session, and all participants completed both experimental tasks, though the order in which they completed the tasks were randomized. Transcranial magnetic stimulation was used to elicit MEPs as a measure of corticospinal excitability throughout the task (Stinear & Byblow, 2003). To address the primary objective, this study explored one main hypothesis: by examining the influence of task nature on corticospinal excitability during mental performance, we hypothesized that, after accounting for the effect of each participants' EMG activity prior to TMS stimulation, the average MEP amplitudes obtained via TMS would be higher for the motor task compared to the perceptual task.

Chapter 4: Methodology

4.1 Participants

This study involves the first use of a comparison of corticospinal excitability between imagined tasks of different kinds. As such, no previous literature exists upon which to estimate expected effect sizes for a power analysis. Our laboratory, however, has performed numerous experiments that assessed corticospinal excitability using TMS, and from this past work a moderate ($f=0.40$) effect size is expected. Therefore, a power analysis for the planned analysis (paired one-tailed t -test) to test between group differences was conducted (G*Power 3.1.9.7) using this effect size. The power analysis showed the required sample to be 15 to achieve a moderate effect assuming an alpha of 0.05 and power of 0.8. Assuming an attrition rate of 10%, the final sample size was 17. Participants were aged 17-60 years with normal or corrected-to-normal vision, in good health (i.e., no history of any neurological injury/disease as reported by the participants), and no contraindications to TMS, determined via the standard screening form (Appendix A). The participants were pseudorandomized (i.e., a process where randomization occurs, but the randomization is done in such a way that equal groups are created) into one of two groups that only differed in the order in which the participant completed the experimental tasks (a motor and perceptual task). Demographic information, including sex, age, and handedness as determined by self-report, was collected to characterize the sample. The study was approved by the Dalhousie University Health Science Research Ethics Board (REB# 2022-6173).

4.2 Questionnaires

Kinesthetic Visual Imagery Questionnaire

The Kinesthetic Visual Imagery Questionnaire (KVIQ) is used routinely to assess motor imagery ability in both healthy and disabled populations (Malouin et al., 2007; see Appendix D)(Malouin et al., 2007). The KVIQ assesses the vividness of both the visual and kinesthetic dimensions of motor imagery and involves both the physical and imagined performance of 5 different simple movements (e.g., simple shoulder flexion). Importantly, application of the KVIQ has shown high reliability in both non-disabled controls and clinical populations (Malouin et al., 2007). This study employed the use of the KVIQ-10, a 10-item version of the KVIQ consisting of 5 movements.

To conduct the KVIQ, the first movement on the questionnaire was physically demonstrated to the participant by the researcher. Following this demonstration, the participant was asked to perform the movement in three different ways; first, to physically perform the movement as had been demonstrated to them. Second, to imagine the movement via visual (third person) imagery, whereby the participant imagined what it looked like to observe someone else performing the movement. Following visual imagery of the movement, the participant was asked to provide a rating on a scale from 1-5 of how clearly they could imagine seeing the movement performed, where a rating of 1 indicated low clarity during imagery and a rating of 5 indicated high clarity (Malouin et al., 2007). Finally, the participants were asked to imagine the movement via kinesthetic (first person) imagery, whereby the participant imagined what it felt like when they performed the movement themselves. Following kinesthetic imagery of the movement, the participant were again asked to provide a rating on a scale from 1- 5, this time of how

intensely they could imagine the feelings associated with performing the movement, where a rating of 1 indicated low intensity during imagery and a rating of 5 indicated high intensity (Malouin et al., 2007). KVIQ results were used to characterize each participant's ability to perform imagery, not as a screening tool.

4.3 Experimental Session Overview

The study consisted of a single 2-hour long session. The first 15 minutes of the session were devoted to an overview of the study, TMS screening (Appendix A), informed consent (Appendix B), motor imagery familiarization (Appendix C), and the KVIQ (Appendix D). The following 30-45 minutes were used to set the participant up for TMS which included establishing the participant's motor "hotspot". Immediately following, participants completed the two experimental tasks that each contained two blocks, with the tasks being a trajectory tracing task and an ISL task and the blocks consisting of motor imagery and PP. Each task started with imagery blocks and ended with one PP block, with rest periods of 1 minute distributed between each block and a 3-minute rest period between experimental tasks, during which the participant was given instructions for the following experiment (Figure 8A). All trials lasted 1500ms. During motor imagery blocks, single pulse TMS was delivered halfway through a given trial (roughly 750ms) (see Figure 8B). The experimental tasks lasted approximately 60 minutes in total. The order of task completion was randomized to account for potential order effects. The tasks varied in terms of number of trials and their duration because we sought to maintain their form closely to that of the studies in which they have been used previously in our laboratory, and thus only minimal modifications were made. We took this approach to reduce the potential impact that major changes to the paradigms might

have on the observed results. Participants were debriefed and compensated for their time at the end of the session.

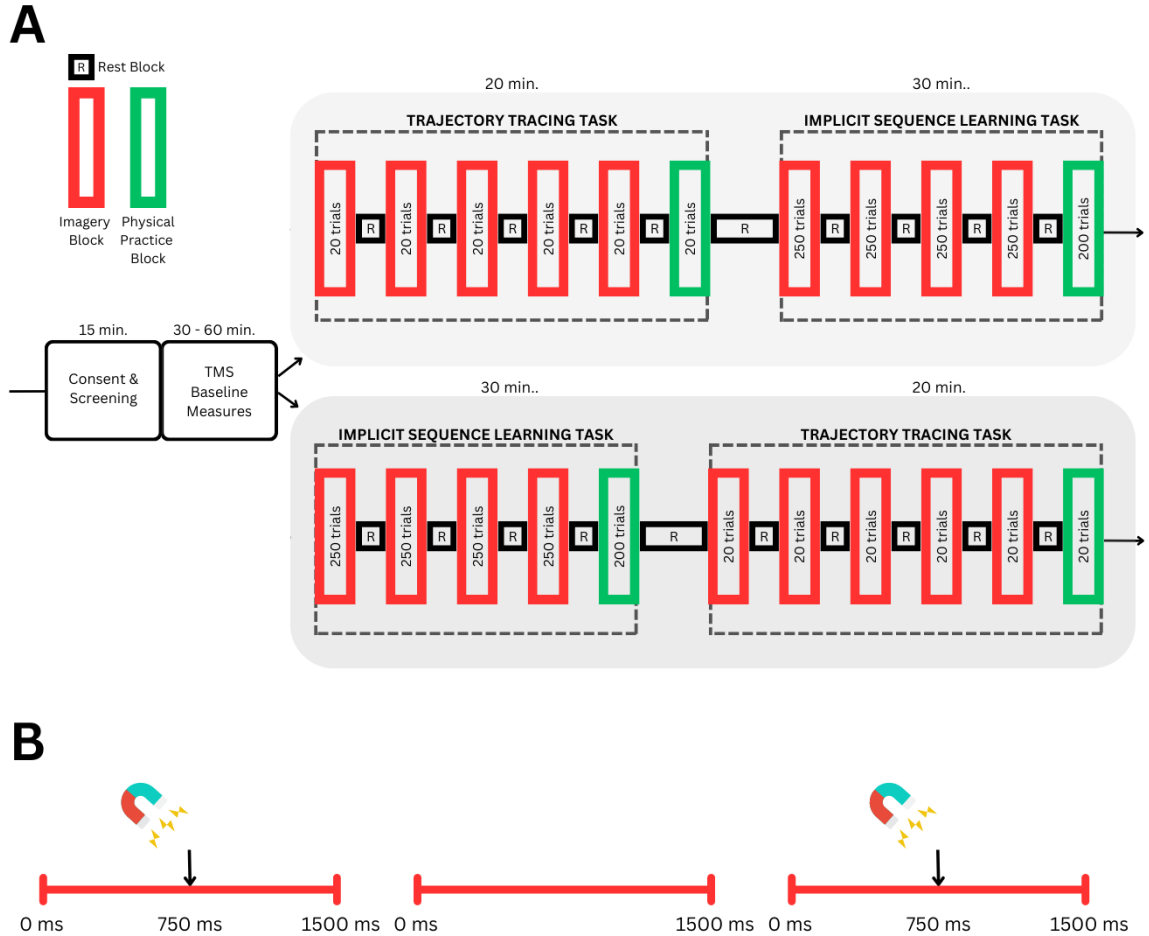


Figure 8. Experimental Block Structure & TMS Timing. (A) The structure and timeline of the experimental session is depicted. Red rectangles represent motor imagery blocks, green rectangles represent PP blocks, and breaks are represented by solid black squares or rectangles with the letter “R” in its middle. The rounded black rectangles show the time estimated for consent and screening, and TMS hot spotting. The content within grey rectangles show the time estimated for the experimental tasks and their blocks, with the top grey rectangle representing Order 1, and the bottom grey rectangle Order 2. The Trajectory Tracing Task contained six blocks consisting of 20 trials. The ISL task consisted of five blocks, with the first four blocks consisting of 250 trials, and the fifth block consisting of 200 trials. All blocks were separated by 1 min of rest. A 3 min rest period was provided in-between tasks to give instructions to the participant before the next task began. (B) The timing and trial type that TMS can occur within the experimental tasks. The red timeline represents the trials in motor imagery blocks and are the only trial types that TMS occurs in the experimental tasks. The magnets represent the application of a single pulse of TMS, and the arrow indicates the point in time that this occurs during

each trial. The middle trial does not contain a magnet and represents the fact that TMS pulses are spaced such that they cannot occur less than 3 seconds apart.

4.4 Task Overview & Apparatus

4.4.1 Experimental Apparatus

Touch Screen

The monitor used to display trajectories to be reproduced by participants was a 24" touchscreen (Planar PCT2485; 1920 x 1080 resolution). The monitor was placed on a table located directly in front of the participant, such that their dominant hand could comfortably reach all corners of the screen, as they sat comfortably upright resting on a chin rest.

Keyboard

The keyboard in this experiment was modified such that the “Z”, “X”, “C”, and “V” keys were replaced with “4”, “3”, “2”, “1” and the “M”, “<”, “>”, and “?” keys were replaced with “1”, “2”, “3”, “4”, creating a mirrored configuration. This mirrored configuration allowed for the index, middle, ring, and pinky fingers of each participant’s *dominant* hand to rest on the keys 1-4, regardless of the participant’s handedness, ensuring that the experimental paradigm was as close as possible between left and right-handed participants (Figure 9).



Figure 9. Implicit Sequence Learning Task Modified Keyboard. A photo depicting how the keyboard was modified for use in the ISL task.

4.4.3 Trajectory Tracing Task

Participants were asked to perform a task that required the observation and imagined reproduction of a complex movement trajectory. They were seated comfortably at a desk with the experimental setup in front of them (Figure 10). The task involved the use of a touch screen monitor that collected the participant's response. At the start of each trial, a white dot moving in a complex trajectory on the display was presented to the participant. Each shape began and ended at a predetermined starting point centered near the bottom of the display. To indicate that the tracing of the shape had ended, participants were presented with a solid red circle at the starting (and ending) location on the screen. Immediately upon completion of the stimulus (that is, as soon as the red circle appeared), the participant was asked to imagine tracing the shape on the touch screen as accurately as possible (blocks 1-5) and subsequently to physically trace the shape on the touch screen in the final (sixth) block. Each of the blocks in this task consisted of 20 trials for a total of 120 trials (100 motor imagery trials and 20 physical execution trials), and participants were given a 1-minute rest between blocks. During this task, different shapes

were presented to the participants - one of the shapes repeated (the shape to be learned) with the other shapes being spatially unique and randomly generated but matching the complexity of the repeated shape. The repeated and random shapes were presented at a 1:1 ratio.

To evaluate within-session performance of the task, performance (obtained via physical execution in the sixth block) on the repeated shape was compared to the random shapes (Ingram et al., 2019). In the motor imagery blocks (blocks 1-5), participants placed the index finger of their dominant hand on the red dot and mentally simulated the trajectory observed as accurately as possible and then lifted their finger to indicate they had completed the trial. To attempt to ensure that participants were performing imagery, the stimulus trajectories were presented such that they animated over a period of 1.5s, and the movement time (the length of time in which participants left their finger on the red circle) was compared to the length of time it took them to trace the shape in the final block to ensure that these times were similar. Previous research has demonstrated that the amount of time spent imagining a movement should match the amount of time required to physically perform the movement (Ingram et al., 2019; Malouin et al., 2008). During the motor imagery trials (blocks 1-5), single-pulse TMS was applied to assess corticospinal excitability (see TMS below). In the final (sixth) block, participants began a trial by placing their finger on the red circle and then physically traced the shape, returning to the red circle to end the trial. Accuracy between the randomly generated shapes and the repeated shapes was compared to provide further evidence that participant's were performing motor imagery in blocks 1-5 as prior research out of our laboratory had

demonstrated better accuracy on repeated trajectories vs. random trajectories (Ingram et al., 2019).

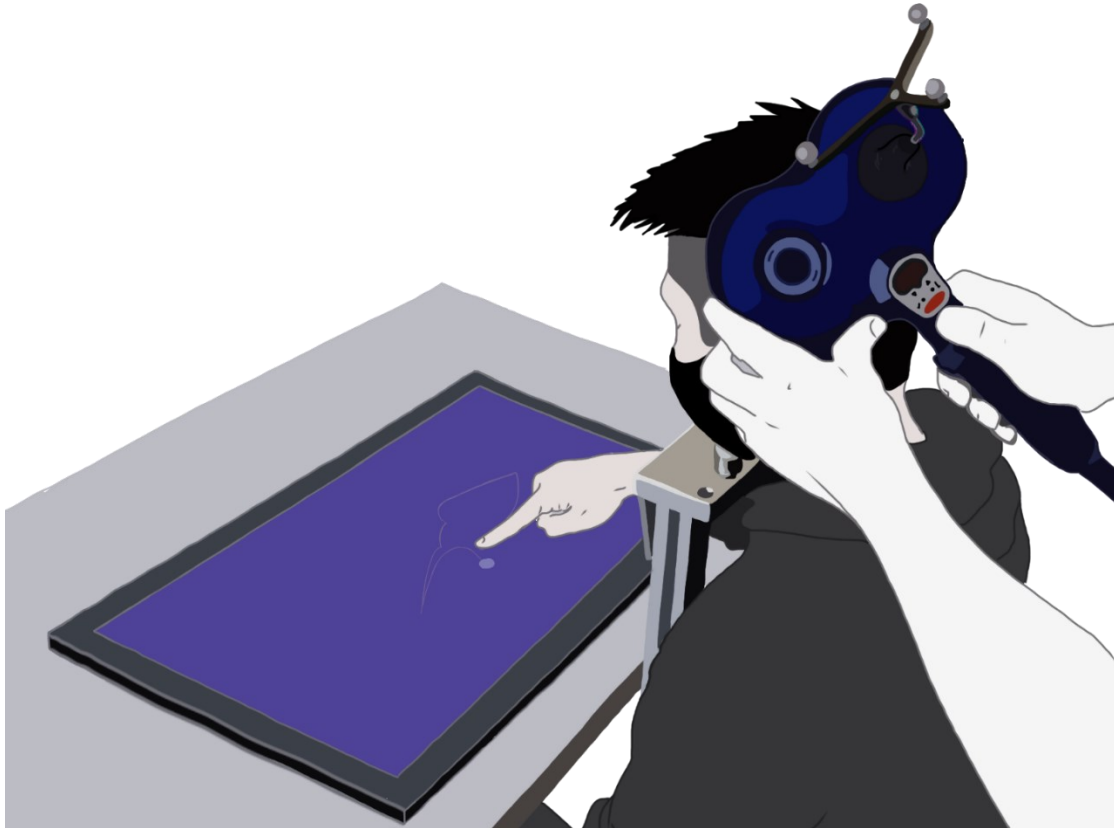


Figure 10. Trajectory Tracing Task Experimental Set-up. A depiction of the trajectory tracing task demonstrating the position of the participant and researcher throughout all motor imagery blocks (Solomon et al., 2022).

4.4.4 Implicit Sequence Learning Task

Participants were asked to perform an imagery-based ISL task (like a serial reaction time task or SRTT), which had been previously used in research conducted by the laboratory (see S. N. Krautner, Gaughan, et al. (2017) for a detailed analysis of the task paradigm) (S. N. Krautner, Gaughan, et al., 2017). Participants were asked to close their eyes and imagine performing seemingly random sequences of keypresses.

Embedded within this seemingly random sequence, however, was a repeated sequence that the individual could learn in spite of not retaining explicit knowledge of having learned it (Destrebecqz & Cleeremans, 2001; Goschke & Bolte, 2012; Kantak et al., 2012). The participant performed the task sitting comfortably with the experimental setup in front of them, which consisted of a keyboard and computer monitor resting faceup on a desk. The participants' non-dominant arm was resting comfortably on their lap, and their dominant hand was placed on a modified keyboard overlying keys '1, 2, 3, 4', as described above. At the start of each trial, the participants were presented with an auditory cue (verbalized number 1-4). After hearing the auditory cue, the participant imagined pressing (blocks 1-4) the corresponding key on the keyboard. For the trials in the motor imagery blocks (blocks 1-4), 72% of keypresses corresponded with the repeated sequence and 28% corresponded with a random sequence. Both sequences consisted of 10 digits, but the repeated sequence was constrained such that no two consecutive digits repeated. The placement of each sequence was randomized within each block, such that the order of repeated and random sequences appeared varied to the participants. Blocks 1-4 consisted of 250 keypresses/trials, and the last (fifth) block consisted of 200 trials, with a 1-minute rest after each block. If participants pressed a button during the training block, an error tone played, and the error response was recorded. Each individual key pressing event lasted 1.5s. During each motor imagery trial (blocks 1-4), single-pulse TMS was applied to assess corticospinal excitability as described in the following section. In a final (fifth) block of the task, participants physically pressed the key corresponding to the number spoken in the auditory cue to obtain RTs for analysis. Trials in this final (fifth) block had random and repeated

elements presented at a 1:1 ratio. As in the prior blocks, an error tone played if participants made an incorrect response. In this final block, participants did not receive brain stimulation.

To assess any within-session performance changes that occurred via imagery-based practice of the task, RTs between responses to repeated and random sequence elements were compared. At the end of the experimental blocks, participants were given a prompt on the computer monitor asking if they believed they had learned a sequence during this task to ensure that any learning that may have occurred was implicit in nature (i.e., the participants were not aware of the repeated sequence and thus could not engage in other forms of practice) by asking participants to respond by pressing “y” or “n” on the keyboard corresponding to “yes” or “no,” respectively. Participants were told that it was okay if they did not think they did. If the participant answered “yes,” they were asked to type the sequence they thought they had learned on the keyboard. These responses were recorded and stored for offline analysis to determine whether participants had explicit knowledge of the repeated sequence, with participants who answered “yes” and correctly identified at least 5/10 sequence elements having their data removed from further analysis.

4.4.5 TMS Procedures

Single-pulse TMS was administered to the cortical representation of the first dorsal interosseous muscle (FDI) muscle in M1, contralateral to the side of the participants’ dominant hand (Kleim et al., 2007). Stimulation was delivered via a 70mm figure-of-eight coil connected to a Magstim BiStim2 system (The Magstim Company, Whitland, UK).Brainsight 2 neuronavigation software was used to guide positioning and

orientation of the coil over M1 (Brainsight 2™; Rogue Research Inc., Montreal, CA). Co-registration of the participant's head to a template MRI scan (MNI152_T1_1mm) was achieved by aligning anatomical landmarks on the participant (i.e., nasion, left preauricular (LPA), right pre-auricular (RPA), glabella and tip of the nose points) to the same points on the template MRI, with further adjustments and scaling achieved using numerous points along the head, including the left, right, front, back and top-most points. For all TMS procedures, the coil was held in close proximity to the skull, with the handle pointing posteriorly and laterally at an angle of 45° to the mid-sagittal line. A 7x7 grid (each grid point 7.5mm apart) was positioned over the template brain, with the center point (3, 3) overlying the cortical representation of the flexor muscles of the forearm. Stimulator intensity was set to 42% of the stimulator's maximum output, and different locations on the grid were stimulated to determine the area and stimulus output intensity of each participant's RMT. A maximum stimulator output intensity of 50% was not surpassed during the experimental session, as stimulation at an output greater than 50% on the Magstim BiStim² system often resulted in activation of musculature in the head/face regions that could cause discomfort after prolonged periods of time. Since the stimulator intensity was set to 120% of the RMT value to elicit MEPs during the experimental task, an RMT at 42% or greater exceeded the 50% stimulator intensity threshold; if a participant was not reliably responsive to stimulation under 42% intensity, they were excluded from further participation.

Resting motor threshold was defined as the minimal stimulation intensity at which the target muscle produced an MEP with amplitude $\geq 50 \mu\text{V}$ in a minimum of five out of ten trials. Beginning at point 2,2 stimulation was delivered at increasingly lower intensities

until 5/10 MEPs could no longer be achieved. Once this was the case, the same process occurred at grid points neighboring 2,2 to test if any location yielded 5/10 MEPs at a lower intensity. This process continued until a grid point was isolated, with all points around it unable to produce 5/10 MEPs at a lower intensity. Once location and stimulation intensity were determined, the experimental task began. During each experimental task, 50 single pulses of TMS were applied at 120% RMT, resulting in a total of 100 total single pulses of TMS over both tasks. During the imagery blocks of each task (described in detail above), single pulse TMS was delivered halfway through a trial (roughly 750ms) to maximize the probability that stimulation occurred while the participant was performing imagery (as detailed in Figure 7). With the exception of single-pulse TMS for hotspot localization and determination of RMT, during which the stimulator was under manual control, delivery of stimuli was automated based on a custom script written in Python 3.0 and using associated hardware (Spike2 v 7.09a, 1902 amplifier and Power 1401; Cambridge Electronic Design, UK).

4.4.6 Electromyography

Motor-evoked potentials were obtained from the FDI muscle using TMS. The FDI, an abductor of the index, middle and ring fingers, was located by palpating the muscle on top of the hand and between the metacarpal of the index finger and thumb while the participant repeatedly flexed their index finger (i.e., finger abduction). Once located, two surface EMG electrodes were placed on the skin overlying the FDI muscle with a 1 cm interelectrode distance and another was placed on the olecranon process to act as a ground. To ensure minimal impedance of the recorded signal and improved adhesion of each electrode, the sites for each electrode were prepared by gently abrading

the skin with NuPrep skin gel (Weaver and Company, Aurora, CO) and then cleaned using an alcohol swab. Electromyography was collected throughout both blocks of the experimental task using Spike2 software (Spike2 v 7.09a, 1902 amplifier and Power 1401; Cambridge Electronic Design, UK) sampled at 1000 Hz with a bandpass of 1-500 Hz.

4.5 Data Analysis

4.5.1 MEP Analysis

The primary outcome measure of this study was the comparison of MEP amplitude (i.e., corticospinal excitability) between tasks. The EMG data obtained during the session was exported to a CFS file from Spike2 and rectified to isolate the envelope of muscle activity. Background EMG was obtained by calculating the mean EMG activity during a 1s window prior to the onset of stimulation during imagery trials. The EMG threshold was defined as EMG activity that was less than 4 times the median absolute deviation of the median EMG signal during the 1s window prior to the onset of stimulation; any EMG activity surpassing this threshold in the imagery block was excluded from analysis. In addition, only MEPs with a value of 60 μV or greater were considered for further analysis. This decision was based on the fact that a MEP is defined as 50 μV during TMS hot spotting, and we expected MEPs to be larger than 50 μV when participants were stimulated at 120% of RMT. If more than 40% of trials were removed from analysis due to excessive background EMG activity or inadequate MEP amplitude, the participant was excluded from further analysis.

The raw EMG signals were processed using custom R scripts that our laboratory had developed and previously used to analyze Spike2 data. These scripts determined the

peak-to-peak amplitude of MEPs by placing a set of cursors 10ms before and 50ms after the TMS pulse to identify the MEP window. Subsequently, the peak-to-peak amplitude, which reflected the difference between the maximum and minimum values of the EMG signal during the specified time period, was calculated and returned by the scripts. This approach accounted for both the conduction time and duration of the MEP. The cursors were visually inspected to verify that the negative and positive peaks related to the MEP were captured and that any artifact related to the TMS pulse was excluded. Since the expected pattern for the standardized MEPs was peak-valley, trials in which the script-determined minimum value of the MEP occurred before the maximum value were inverted (i.e., mirrored around the horizontal axis) such that the minimum became the maximum and the maximum became minimum. As detailed below in the *Statistical Analysis Section*, participant MEPs were represented as z-scores for ease of interpretability after individual variability in participant EMG activity immediately prior to TMS stimulation was accounted for.

4.5.2 Accuracy and Reaction Time Analysis

To ensure that participants were performing motor imagery, several measures specific to each task were recorded and analyzed. In the motor task, stimulus trajectories were presented such that they animated over a period of 1.5s, and the movement time – the time that participants held their finger on the touch screen – was recorded, and the average movement times between motor imagery and physical execution trials were compared as research supported the notion that motor imagery and physical execution of a task took the same amount of time (Ingram et al., 2019; Malouin et al., 2008). In addition, the accuracy of participant responses in the physical execution block of the

motor task was recorded and determined by calculating the point-by-point distance (in pixels, Px) between the stimulus trajectory and the participant-generated trajectory. The total, average and variability of this distance were calculated to characterize accuracy for each trial. To further verify that participants were performing imagery in the motor task, the accuracy on the repeated trials was compared to the random trials as previous research had shown higher accuracy for repeated than random task elements (Ingram et al., 2019).

In the perceptual task, RT was determined by the amount of time (in milliseconds) it took the participant to press a given key in response to the number spoken in the auditory cue for trials in the physical execution block. To verify that participants were performing imagery in the perceptual task, the RTs on repeated sequences were compared to the RTs for random sequences as previous research had shown higher accuracy for repeated than random task elements (S. N. Kraeutner, MacKenzie, et al., 2016). To control for other forms of practice (e.g., verbal rehearsal) in the perceptual task, it was confirmed that any potential learning that may have occurred was implicit in nature (i.e., the participants were not aware of the repeated sequence and thus could not engage in other forms of practice) by asking participants to respond to the question “Do you think you learned a sequence during this task?” by pressing “y” or “n” on the keyboard corresponding to “yes” or “no”, respectively. Participants were told that it was okay if they did not think they learned a sequence. If the participant answered “yes”, they were asked to report the sequence they learned, and these responses were recorded and stored for offline analysis to determine whether participants had knowledge of the repeated sequence, with participants who answered “yes” and correctly reported more

than 50% of the sequence (i.e., 5 consecutive sequence elements) being excluded from further analysis. It was crucial to remove participants with explicit knowledge of the sequence as not doing so could have introduced a confounding variable in that we would not have known if these participants had acquired the sequence via their imagery-based practice or if a different learning strategy amenable to practice when a participant had explicit knowledge of the sequence (e.g., verbal rehearsal) could be used. To control for anticipatory responses and outliers in the physical practice block of the perceptual task, RTs for trials that occurred before 100 ms or after 1300 ms as well as RTs for trials in which an incorrect response was provided were also removed from analysis, a process consistent with prior work (S. N. Kraeutner, Ingram, et al., 2017). In the perceptual task, participants that made physical responses greater than 2% of the time across motor imagery trials were excluded from further analysis.

In summary, the data presented above were collected to assess within-session changes in performance. The objective of evaluating these changes was to provide evidence that participants were engaged in the imagery task. Prior studies in our laboratory had shown that this specific task paradigm was associated with improvements in performance within a single session. Therefore, the absence of any such improvement during the session would have been a cause for concern.

4.5.3 Statistical Analyses

The primary outcome measure of the study was the comparison of the magnitude of the MEP amplitudes (i.e., corticospinal excitability) between the two tasks. The MEPs recorded during the imagery blocks of each task were characterized by task and modelled

to account for participant variability in EMG activity prior to TMS stimulation, as detailed below.

To ensure the project was feasible and within scope for an MSc new experimental tasks were not created; rather, the ISL and Tracing Trajectory Tasks were selected as our perceptual and motoric tasks, respectively, as their paradigms have been well established in previous work in our laboratory, and both were deemed appropriate to address the study's objective (Ingram et al., 2019; S. N. Kraeutner, Gaughan, et al., 2017; S. N. Kraeutner, Keeler, et al., 2016; S. N. Kraeutner, MacKenzie, et al., 2016). The ISL and Tracing Trajectory Tasks were kept as close as possible to their original forms as any alterations could change fundamental attributes of the tasks, which would reduce our ability to determine whether the presence or absence of an effect is expected or unexpected, given the results from previous literature. However, an unavoidable result of this choice was the two tasks varied in their number of trials, blocks, and total duration. Therefore, only a subset of MEPs was selected from each task to ensure consistency in the number of MEPs analyzed across the two tasks given their varying durations. Specifically, in the Tracing Trajectory Task (i.e., the motor task), MEPs were selected pseudorandomly across all imagery blocks such that they matched the number of MEPs recorded within the 25 min timeframe of the perceptual task. For example, participants will have 50 measures of MEP amplitude upon completing the motor task. If a participant took 25 min to complete the motor task, and they only had 30 measures of MEP amplitude within the first 25 min for the perceptual task, then only 30 of the 50 MEPs from the participant's motor task data would be used in calculating the average MEP from the motor task for analysis. In this specific example, these 30 trials would be

pseudorandomly selected across all motor imagery blocks in the motor task such that six measures of MEP amplitude would be selected per block (30 MEPs ÷ 5 imagery blocks = 6 MEPs per block). Selecting MEPs pseudorandomly across all blocks ensured that the sample of MEPs selected was unbiased, and helped account for potential fatigue effects as previous works in our laboratory has shown that longer bouts of continuous imagery corresponded with decreased corticospinal excitability (Lee et al., 2021).

From these participant averages, task and order averages could be determined, and a linear mixed-effects model (LME) was employed using lme4 (version 1.1.34) to assess the factors impacting MEP amplitude between tasks, with t-values used to make inferences about the fixed effects. The independent variables of task type (with levels *motoric task* and *perceptual task*) and the median absolute deviation of the FDI EMG signal were incorporated into the model as fixed interaction effect. The random effect of the model was the independent interaction term nested within participant. Doing so allowed MEP amplitude to be modeled using task as an isolated independent variable while accounting for the effect of EMG activity in the FDI. The MEP amplitudes were then z-scored for ease of interpretation prior to modelling. All statistical analyses were conducted using a custom R script with an a priori alpha of $p < 0.05$ denoting significance.

Chapter 5: Results

5.1 Participant Demographics

A total of 25 participants took part in the study. In 2 participants RMT could not be established, 1 participant was excluded due to having explicit knowledge of the sequence (i.e., recalling at least 5/10 repeated sequence elements) in the ISL task, 2 participants were excluded due to having too many trials dropped as their EMG data surpassed the threshold, 2 participants were excluded due to withdrawing from the study, and 3 were excluded due to technical difficulties preventing completion of both experimental tasks. With these participants removed, 15 participants (7 = female, 15 = right-handed, 7 = Order 1) remained. The age of participants ranged from 18-41 (M = 25.8, SD = 5.3), and participants self-reported being able to perform motor imagery based on the kinaesthetic scores on the KVIQ (M = 19.3, SD = 5.8).

5.2 EMG/MEP Data

EMG data was filtered and MEPs were calculated as described in the methods. 225 (11.4%) trials were dropped from the imagery data due to meeting the atypical criteria for MEPs or exceeding the threshold for acceptable EMG activity while at rest. After the data was cleaned and filtered, a total of 1741 (88.6%) of trials remained for further analysis. 51 (22.7%) of excluded trials were from the motoric task and 174 (77.3%) from the perceptual task.

5.3 Accuracy & Reaction Time

In the motoric task, mean accuracy for the repeated and random trajectories were 105.5 mm \pm 19.8 mm and 110.4 mm \pm 26.3 mm, respectively (Figure 11). In the

perceptual task, mean RT for the repeated and random sequences were $756.6 \text{ ms} \pm 25.1 \text{ ms}$ and $783.0 \text{ ms} \pm 21.2 \text{ ms}$, respectively (Figure 12).

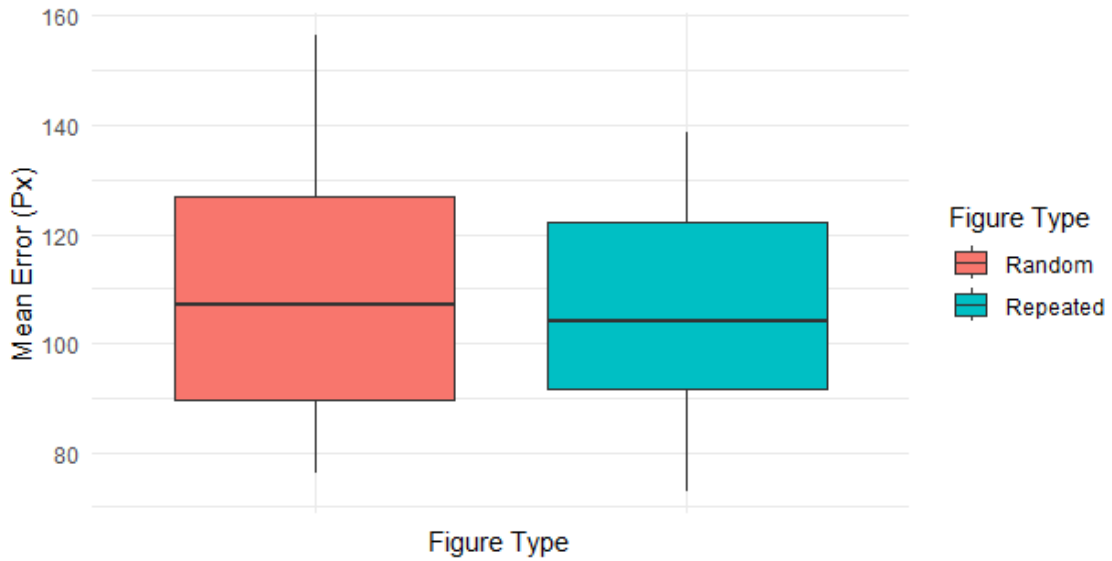


Figure 11. Visualization of Response Accuracy by Figure Type. Box plot showing the mean error (Px) for the repeated and random trajectories. The median error of each figure type is indicated by the solid horizontal line inside each box, 1st and 3rd quartiles by the boundaries of the boxes, and ranges by the vertical lines extending from the boxes, and outliers by any points not contained within the box.

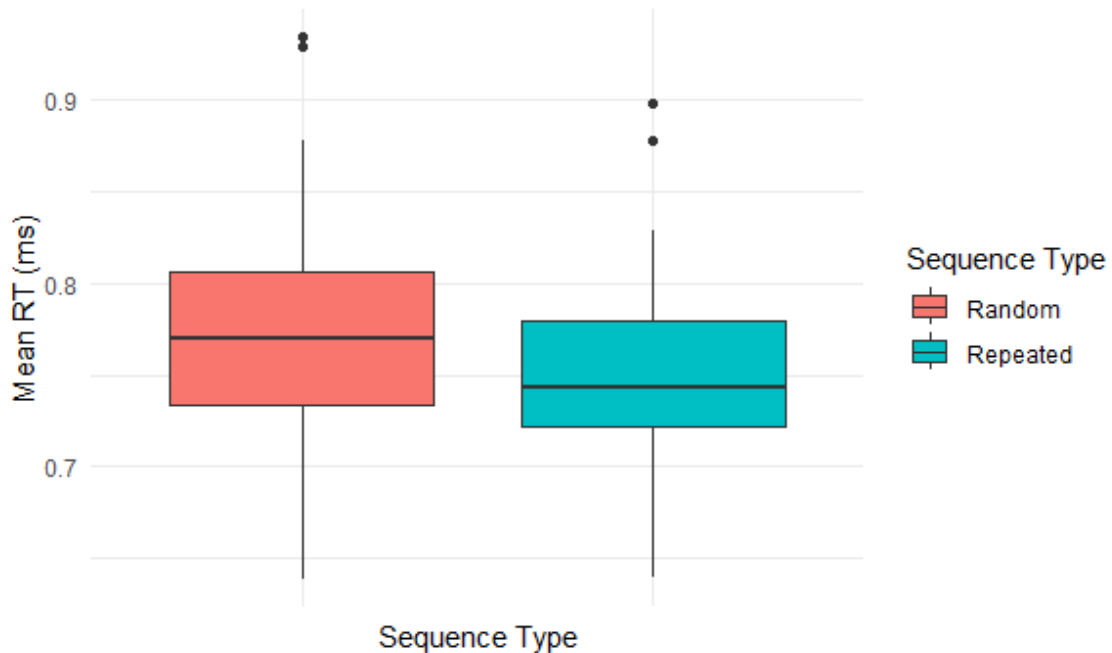


Figure 12. Visualization of Reaction Time by Sequence Type. Box plot showing the mean RT (ms) for the repeated and random sequences. The median error of each sequence type is indicated by the solid horizontal line inside each box, 1st and 3rd quartiles by the boundaries of the boxes, and ranges by the vertical lines extending from the boxes, and outliers by any points not contained within the box.

5.3.1 Effect of task on MEP amplitude

Significant effects were examined by plotting the predicted effects of the model, and effect sizes were estimated using Cohen's d . The LME analysis resulted in several findings, with detailed test results summarized in Table 1. There was a significant positive relationship between participant's pre-pulse EMG amplitude and their average MEP amplitude, ($t(19.90)=5.121, p<0.001$), where increased pre-pulse EMG amplitude corresponded with increased MEP amplitude. The effect size of this relationship was large, with $d = 1.17 [0.58, 1.75]$, which can be interpreted as meaning that as muscle activity increased before stimulation onset, there was a strong and noticeable increase in MEP amplitude. There was also a significant effect of task on participants' MEP

amplitude ($p < 0.001$), with a strong effect size of $d = -1.31$ $[-2.00, -0.58]$. Since the perceptual task was coded as 1 in the model and the motoric task was coded as 2, this strong effect suggests that the perceptual task led to markedly lower MEP amplitudes when compared to the MEP amplitudes recorded in the motoric task. The interaction term between task type and pre-pulse EMG amplitude was nonsignificant ($p > 0.05$) and had a small effect size, $d = 0.12$ $[-0.41, 0.64]$. Pairwise comparisons using estimated marginal means revealed the average MEP amplitude in the perceptual task was significantly lower than in the motoric task ($t(14) = -4.899$, $p < 0.001$) as visualized in Figure 13.

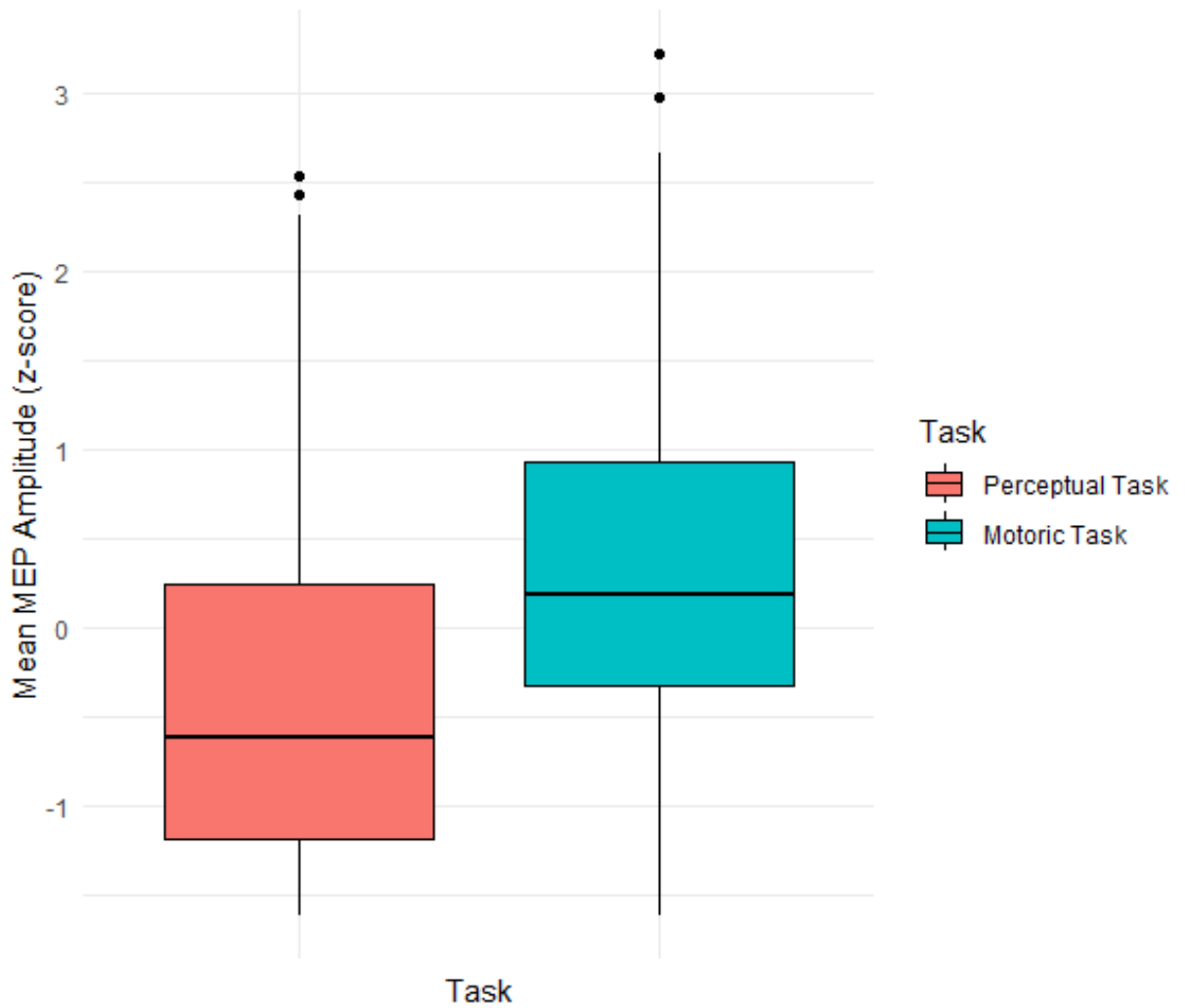


Figure 13. Visualization of Task Effect on Mean MEP Amplitude (z-score). The median MEP amplitude of each figure type is indicated by the solid horizontal line inside each box, 1st and 3rd quartiles by the boundaries of the boxes, and ranges by the vertical lines extending from the boxes, and outliers by any points not contained within the box.

Table 1: Linear mixed effects omnibus test findings, z-scored.

<i>Model Parameter</i>	<i>Coefficient</i>	<i>Standard error</i>	<i>Confidence interval (95%)</i>	<i>T-statistics</i>	<i>P-value</i>	<i>Cohen's d</i>
<i>Intercept</i>	0.07077	0.19816	-0.47, 0.33	-0.357	0.726330	-0.096
<i>Pre-pulse EMG</i>	0.09506	0.01856	0.06, 0.13	5.121	5.29e-05	1.175
<i>Task</i>	-0.729	0.149	-1.05, -0.41	-4.899	0.0002	-1.307
<i>Pre-pulse EMG * Task</i>	0.01735	0.03921	-0.06, 0.10	0.442	0.665136	0.118

Chapter 6: Discussion

6.1 General Results

The present study aimed to better understand the mechanisms underlying motor imagery, specifically the role of the M1 in motor imagery and the influence of task nature on motor learning via imagery. This was accomplished by having participants perform a motoric and perceptual task using motor imagery. All participants completed both tasks, but the order in which tasks were completed were randomized to account for any order effects. The hypothesis was that, after accounting for the effect of each participants' EMG activity prior to TMS stimulation, the average MEP amplitudes obtained via TMS would be higher for the motor task compared to the perceptual task.

Over the course of the experiment, participant performance on the repeated task elements of both tasks (i.e., the repeated trajectory in the motoric task and the repeated sequence in the perceptual task) was generally better than their performance on the random task elements. These results are consistent with prior literature using these tasks, where participants had better accuracy (in the motoric task) and a faster reaction time on repeated sequence elements (in the perceptual task). Given that these general improvements were seen on repeated and not random task elements, it suggests that participants were effectively using motor imagery to improve task performance, an expected trend consistent with prior work (Ingram et al., 2019; S. N. Kraeutner, Gaughan, et al., 2017).

Analysis of corticospinal excitability obtained via TMS revealed crucial insights into the influence of task nature on our understanding of motor imagery. Notably, and *imperative* to the interpretation of the results, was the inclusion of pre-pulse EMG

amplitude in the model. If we had not accounted for pre-pulse EMG and instead only modelled the effect of task type, then any conclusions drawn from the model may have been erroneous as it is possible that another variable or factor, like pre-pulse EMG, better explained the effect. Therefore, by including pre-pulse EMG in the model while still having a significant effect of task type, we can conclude that task type independently influenced MEP amplitude because we have accounted for the unique effect and influence of pre-pulse EMG amplitude on MEP amplitude. In addition, the lack of either a significant or meaningful interaction between task type and pre-pulse EMG amplitude, suggesting that the effect of task type on MEP amplitude was not mediated by the pre-pulse EMG amplitude, and similarly, that the effect of pre-pulse EMG on MEP amplitude was not mediated by task type. In other words, each predictor (i.e., task type and pre-pulse EMG activity) exerted their influence on MEP amplitude independently. This lack of interaction effect is visualized in Figure 14. Given the results of these models, the study hypothesis was confirmed: the data indicate that task nature influences corticospinal excitability during motor imagery, and specifically that the average MEP amplitude values, and thus corticospinal excitability, is higher for the motoric task compared to the perceptual task.

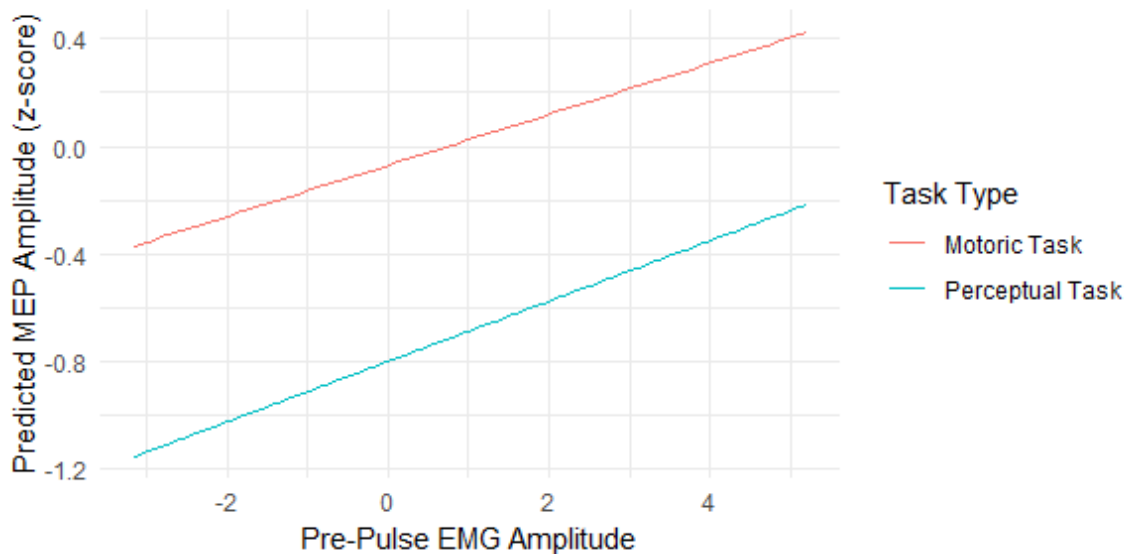


Figure 14. *Lack of Interaction between Model Predictors.* The parallel lines illustrate the lack of interaction effect between Task Type and Pre-Pulse EMG Amplitude on the predicted MEP amplitude in the model, highlighting that each predictor variable's influence on MEP amplitude is not mediated or changed by the value of the other.

6.2 Main Findings

Results of the study showed that the imagined task had a significant influence on MEP amplitude, with MEP amplitude being significantly larger in the motoric task than the perceptual task. Importantly, these results were accompanied by a lack of significant interaction between the participant's pre-pulse EMG levels and the task, which suggests that the influence of task on MEP amplitude is not a function of pre-pulse EMG amplitude. Moreover, the findings agree with the general notion that task influences corticospinal excitability, where previous research has for instance demonstrated a difference in corticospinal excitability due to the task's complexity (Roosink & Zijdwind, 2010) and imagined force (Helm et al., 2015). However, the present study proposes novel ways to view and evaluate the nature of an imagined task (i.e., how

“motoric” and “perceptual” the task is) and is the first to directly compare the effect of task on corticospinal excitability in a repeated measures design. As such, it is difficult to situate the study amongst the existing literature as the body of existing literature tends to view a task’s nature in terms of complexity, which is a nebulous concept to operationalize.

There are many factors to consider when unpacking why there would be an influence of task on corticospinal excitability and why performance of more motoric tasks would have increased excitability relative to more perceptual tasks. First is the involvement of M1, and in what specific circumstances it is typically involved. For instance, one could intuitively argue for larger MEPs in motor tasks compared to perceptual ones, given the distinct role of the M1 in motor tasks as opposed to perceptual ones. However, the purpose of the study was to elucidate how critical the nature of a task is in decoding the workings of motor imagery. It is tempting to argue that motor imagery leans more towards being perceptual since inhibiting M1 during an ISL task does not impair performance (S. N. Kraeutner, Ingram, et al., 2017), yet doing the same with the IPL does lead to an impairment in performance (S. N. Kraeutner, Keeler, et al., 2016). While this doesn't conclusively denote motor imagery as predominantly perceptual, it underscores the likely importance of the IPL to motor imagery performance. Further, the ability to learn despite M1 inhibition does not rule out motor imagery being motoric in nature. In fact, by virtue of the motoric task eliciting increased MEP amplitude, the present study clearly demonstrates that M1 plays a role in imagery, a detail that may have been overlooked in previous studies that used more perceptual tasks (i.e., any SRTT or its variant) and thus may be biased to eliciting brain activation patterns consistent with these

tasks (Janacsek et al., 2020) as opposed to that observed with more motoric tasks (Boe et al., 2012). While the brain activation patterns noted result from physical performance of the tasks, they notably show preferential activation of cortical motor and pre-motor regions (e.g., M1, supplementary motor area) in the motor tasks. The influence of task then is a nuance that is essential for future researchers to appreciate, as further investigation of the effect of task and role of M1 in imagery will provide a more comprehensive understanding of brain function during motor imagery. Indeed, future research could provide key insights into the mechanism(s) of motor imagery and the brain regions that sub-serve it by isolating the contributions of M1 and the IPL via inhibitory stimulation during the trajectory task performance. Such a study would shed more light on the significance of these brain regions, building upon the foundation that the current work established regarding task importance, while simultaneously investigating the effector dependent and independent characteristics of imagery.

6.3 Implications for Theories

The results of the present study have several implications for the existing motor imagery theories. Specifically, attributing some of the difference observed in MEP amplitudes between the two tasks to imagery would suggest that imagery of more motoric tasks preferentially activate M1, a key structure in movement and motor learning, much the same way that it does in motor execution. Hence, this would support the notion that similar brain structures are used in imagery and execution as proposed by the MST and MET which converge on functional equivalence. While this doesn't disprove the other theories, as evidence of absence can't be taken as absence of evidence, it suggests that they don't complete the picture. However, nor would this finding propose that MST

is the “correct” theory, as the mechanisms proposed in MST, and functional equivalence more broadly, remain too ethereal to draw meaningful inference about the specific mechanisms by which motor imagery functions. Instead, the present study’s results suggest that the task used to evaluate imagery has an influence on properties such as corticospinal excitability as measured via MEPs. As detailed above, it is not surprising that MEP amplitude was facilitated during performance of the more motoric task given preferential activation of M1 (and other motor regions) observed during performance of such tasks. That MEP amplitude was not facilitated during performance of the more perceptual task is evidence that drawing conclusions about the nature of motor imagery from studies using such tasks in isolation lead to bias in our understanding of motor imagery. As such, these findings open an exciting new area of research in the field. Researchers can now explore the function of specific brain regions by using more motor-focused tasks. For instance, if inhibiting the M1 during a motor task doesn't affect learning through motor imagery but inhibiting a more perception-focused region (like the IPL) does, it suggests that motor imagery is primarily perceptual in nature. On the other hand, if inhibiting M1 doesn't hinder learning via motor imagery, it indicates that motor imagery functions similarly to actual motor execution, aligning with MST and MET.

6.4 Implications for Rehabilitation & Clinical Use

While there is conflicting evidence surrounding the sole use of imagery as an effective tool for neurorehabilitation and learning more generally in the absence of physical practice, there is evidence supporting it leading to improved functional outcome in stroke patients when combined with other therapies (Barclay et al., 2020). Moreover, recent work from our laboratory has suggested that motor imagery alone is capable of

driving learning in the absence or near absence of physical practice (Ingram et al., 2019; S. N. Kraeutner, MacKenzie, et al., 2016). As such, the study's findings also have implications for applied uses such as rehabilitation after stroke, treatment of movement disorders like Parkinson's, and occupational training. For instance, the study's findings seem to suggest that the mental rehearsal of more motoric tasks could yield improved performance gains over less motoric tasks by leading to a larger increase in corticospinal excitability, with tasks like the trajectory tracing task considered more motoric relative to the ISL task, with the former emphasizing execution of actions as opposed to goal selection and action planning. If such improved performance gains coincide with increased corticospinal excitability, it implies that prescribing practice via imagery will yield improved results, or perhaps only yield results for certain tasks. If motor imagery mainly influences the perceptual end of the spectrum (i.e., if its mechanisms are primarily perceptual), then we wouldn't anticipate improvements in motor outcomes from motor imagery training. This is because it wouldn't directly affect execution; instead, its effects would be limited to goal selection and planning. Conversely, if motor imagery is found to significantly affect the motoric end of the spectrum (indicating its mechanisms lean more towards motor functions), we would expect training in motor imagery to impact all phases of motor execution, from goal selection to the execution of the action itself. Regarding neurorehabilitation, this could justify more extensive research into rehabilitation programs that incorporate remote practice via imagery to recover function in skills adjacent to the trajectory tracing task such as drawing or writing. Rehabilitation programs of this sort would be a boon for clinicians and those recovering from stroke as imagery can be performed in more locations than physical practice and when physically

practicing is not possible owing to fatigue or in the case of paralysis resulting from the stroke. In addition, the study's implications for occupational training are similarly exciting. As in the clinical applications, the present findings could lead to program implementation optimized toward certain types of skills while acknowledging that other kinds of motor tasks may be less effectively practiced mentally.

Although the implications of the study's findings are bountiful and exciting, they are purely speculative as the present findings shed light on an uncharted avenue for motor imagery research. Yet, one thing remains certain: evidence or support for the mechanisms or nature surrounding motor imagery derived from tasks like the ISL used in the present study should be interpreted with caution. And while the present study is not without its limitations, which are unpacked in detail below, it is evident that the task itself has a significant impact on outcomes such as corticospinal excitability. As such, not only is it critical for future motor imagery research to account for the potential effect of task when considering experimental design, but it is also imperative that further research be conducted on the properties of a task which could elicit the difference in MEP amplitudes observed in the present study.

6.5 Limitations

The present study is not without its limitations. It is possible that the muscle used to calculate and evaluate MEP data in the present study, the FDI, poses a limitation. It is possible that using muscles more directly involved in each specific task, for instance the anterior deltoid in the trajectory tracing task or flexor digitorum superficialis in the ISL task, would paint a more accurate picture when comparing the difference in MEP amplitude between the two tasks. Although prior research has demonstrated observable

changes in MEP amplitude when imagery is performed for tasks that would not predominantly activate the FDI (Lee et al., 2021), and neither of the selected experimental tasks predominantly use the FDI, the use of the FDI presents a possible confound and alternative explanation for the results found. While brainstorming the experimental design, we planned to have a different muscle for each task, but the logistics of having to find a TMS hotspot for two different muscles and alternate electrode placement during the experimental session was prohibitive, leading to the decision to use the FDI. Nevertheless, future research investigating task nature through investigating MEP amplitude should use target muscles that are more specific to a muscle that is predominantly active during the respective task to build a robust case for any findings made.

Another limitation related to the task's design is the specific tasks used, with those being the trajectory tracing task (i.e., the motoric task) and ISL task (i.e., the perceptual task). While similar in the sense that both tasks incorporated repeated and random task elements, they differ in block structure, number of trials, and duration, presenting a potential confound in comparing differences in MEP amplitude between the tasks. Specifically, the difference in task duration may have had led to boredom in the longer task or mind wandering, leading to a lapse in sustained imagery and contributing to the observed difference in MEP amplitude. Like the choice of muscle, the rationale for selecting these tasks related to feasibility and the fact that the tasks were valid constructs used in previous studies in our laboratory. Nevertheless, future research comparing task influence on MEP may wish to design or select tasks that are more similar in their number of blocks and trials as well as overall duration.

Another limitation may pertain to the lack of learning investigated in the present study. While the results suggest learning took place, as evidenced by the generally improved accuracy and decreased reaction times for repeated elements in the trajectory tracing and ISL tasks respectively, to adequately assess learning would require a retention test performed at least 24 hours post-training to allow for off-line learning to occur. It has been the experience of the laboratory that multi-day TMS studies are logistically challenging to recruit for and conduct, contributing to the decision to conduct the experiment in a single session at the cost of this limitation. Although the current study did not directly evaluate learning, there were noticeable improvements in the within-session performance for the variables we expected to see improvements in (i.e., decreased mean error and mean RT on repeated task elements compared to random task elements). Given that improvements on these variable scores have been previously demonstrated in learning studies conducted by our laboratory using the same experimental tasks, this suggests that participants effectively engaged in imagery as a learning modality. Regardless, investigating learning through multi-day testing would further illuminate the effect of increased corticospinal excitability on the efficacy of learning and how task nature influences this effect.

Chapter 7: Conclusions

This exploration into the mechanisms of motor imagery, particularly surrounding the influence of task nature, has unveiled curious insights into the mechanisms of motor imagery. Our study definitively underscores the influence of task nature on corticospinal excitability, with elevated excitability in motoric tasks compared to a perceptual one. This lends support to prevailing theories like MST and MET that posit a functional equivalence between motor imagery and execution, even though these theories may not provide an exhaustive explanation. Crucially, the implications of our findings extend beyond the realm of research. They hold promise for applied settings, especially in the field of neurorehabilitation. If motor imagery can effectively harness the brain's motor systems in a manner akin to motor execution, it could revolutionize rehabilitation paradigms, particularly for patients recovering from stroke or those grappling with movement disorders. The potential of mental rehearsal in occupational training further underscores the versatility and utility of our findings. However, while the current research has opened exciting new avenues in motor imagery studies, it is not devoid of limitations. The use of the FDI muscle and discrepancies in task structures emphasize the need for even more nuanced research methodologies in future studies. Despite these limitations, the central theme remains unaltered: the nature of the task is paramount in shaping outcomes in motor imagery studies. It is imperative for future research in this domain to be acutely aware of the task's potential effects and to navigate experimental designs accordingly. As we stride forward in understanding the intricacies of the human brain and motor imagery, this research serves as a lighthouse: a beacon that illuminates the path forward while also a warning of the challenges that lie ahead. It is our hope that

this study can act as a foundation upon which future researchers can build, refining our understanding of motor imagery and eventually translating it into tangible benefits for society at large.

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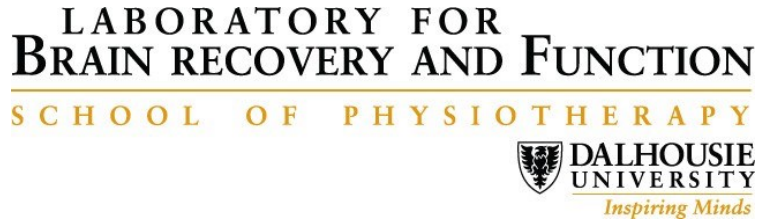
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TRANSCRANIAL MAGNETIC STIMULATION (TMS) SCREENING FORM

Below is a questionnaire used to determine whether potential participants are suitable for research studies using transcranial magnetic stimulation (TMS). Please complete the questions honestly and to the best of your knowledge. This information, as well as your identity, will be kept completely confidential.

Participants Study ID: _____

Participants Age: _____

PLEASE COMPLETE THE QUESTIONS BELOW

	Yes	No
1. Do you have epilepsy, or have you ever had a convulsion or a seizure?		
2. Do you have any hearing problems or ringing in your ears?		
3. Do you have cochlear implants?		
4. Are you pregnant or is there any chance that you might be?		
5. Do you have an implanted neurostimulator (e.g., DBS, epidural/subdural, VNS)?		
6. Do you have cardiac pacemaker or intracardiac lines?		
7. Do you have a medication infusion device?		

<p>8. Have you ever had a fainting spell or syncope (loss of consciousness)? If yes, please describe on which occasion:</p>		
<p>9. Have you ever had a head trauma that was diagnosed as a concussion or was associated with a loss of consciousness?</p>		
<p>10. Are you taking any medications? (please list):</p>		
<p>11. Do you have metal in the brain, skull or elsewhere in your body? (e.g., splinters, fragments, clips, etc.)? If so, please specify:</p>		
<p>12. Did you ever undergo TMS in the past? If yes, were there any problems:</p>		
<p>13. Did you ever undergo MRI in the past? If yes, were there any problems:</p>		

If you answered “yes” to any of the first 7 questions you are not eligible for this study. Please contact the researcher to let them know that you are not eligible; you do not have to tell why you are not eligible.

Please bring a list of your medications to the first study visit.

* TMS screening form is from the International Consensus Guidelines:

Rossi S et. al. (2021). Safety and recommendations for TMS use in healthy subjects and patient populations, with updates on training, ethical and regulatory issues: Expert Guidelines. *Clin Neurophysiol* 132: 26

Appendix B: Consent Form



CONSENT FORM

Project title: Investigating the effect of task nature on corticospinal excitability during motor imagery

Co-Investigators:

Dr. S.G. Boe

Professor

School of Physiotherapy

Dalhousie University

(902) 494-6360

s.boe@dal.ca

H.J. Barr

MSc Candidate

Department of Physiotherapy (Rehabilitation Research)

Dalhousie University

(778) 883-4837

hudson.barr@dal.ca

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Introduction

You have been invited to take part in a research study. A research study is a way of gathering information on a treatment, procedure or medical device or to answer a question about something that is not well understood. Taking part in this study is voluntary. It is up to you to decide whether to be in the study or not. Before you decide, you need to understand what the study is for, what risks you might take and what benefits you might receive. This consent form explains the study.

Please read this carefully. Take as much time as you like. Mark anything you don't understand or want explained better. After you have read it, please ask questions about anything that is not clear.

The researchers will:

- Discuss the study with you
- Answer your questions
- Keep confidential any information which could identify you personally
- Be available during the study to deal with problems and answer questions

You are being asked to take part in this study because you replied to our advertisement and meet the study requirements.

Purpose and Outline of the Research Study

We learn and improve skills when we practice them. Practice can be done by physically repeating the task or by imagining task performance using a process called motor imagery (MI). Some of the evidence supporting motor imagery as a method for learning and practicing skills is that practice using motor imagery leads to the improved performance of a skill compared to no practice at all.

However, we are not sure how learning and practicing using motor imagery works and if the type of motor skill matters. It could be that certain motor skills are more effectively learned using motor imagery than other motor skills are. Luckily, brain activity can be measured and there is evidence to support that higher levels of measured brain activity suggest more motor learning is occurring and lower levels of measured brain activity mean less motor learning is occurring. The purpose of the current study is to examine if brain activity differs between different types of motor tasks when performing motor

imagery. The information gathered in this study will further our understanding of how we learn motor skills and will help us design better training programs for sports, work skills, and rehabilitation.

Who Can Take Part in the Research Study

You may participate in this study if you between 17 and 60 years of age, have normal or corrected-to-normal vision (i.e. you wear glasses or contacts) and you have no conditions that would prevent you from participating. We will determine your eligibility for the study using a screening test that we describe below.

What You Will Be Asked to Do

Screening

If you decide that you want to be in this study and sign this consent form, you will be randomly (like the roll of a die) placed into one of two groups that we describe in the next section. You will then be asked to complete some questionnaires to see if you can take part. This is called screening. It is possible that the screening results will show that you can't be in the study. The research team will discuss these with you. Importantly, if you do not feel comfortable answering the screening questions, we will withdraw you from the study. You will still receive your honorarium or SONA points if you are withdrawn.

The screening test that will be done is a questionnaire to determine if you can participate in transcranial magnetic stimulation (TMS; described in the next section). We will be using this technique to measure brain excitability (detailed below) during the experiment. This set of questions will take about 5 minutes to complete. The answers to the questions will determine whether or not you have any conditions that could possibly cause you harm if you were to participate in brain stimulation (TMS).

A questionnaire that measures handedness

This questionnaire will measure how right-handed or left-handed you are. We will ask you to complete this questionnaire at the beginning of the study session. To complete this questionnaire, you will be given a list of ten every-day, common, one-handed tasks. You will be asked which hand you use to perform these tasks. This information will allow us to determine whether you are right or left-handed.

Motor imagery familiarization script

This script will provide you information about motor imagery such as what motor imagery is, the kinds of motor imagery that exist, and how to perform motor imagery in this study. We will ask you to read through this script at the beginning of the study session. This will allow you to become familiar with motor imagery prior to performing it.

A questionnaire that measures motor imagery ability

This questionnaire will measure how vividly you are imagining a movement. We will ask you to complete this questionnaire at the beginning of the study session. To complete this questionnaire we will show you how to do a movement, ask you to perform the movement, and then ask you to imagine yourself performing the movement. We will then ask you to rate how well you imagine performing the movement compared to actually performing it. This information will allow us to determine how well you can do motor imagery.

Muscle activity

Activity in your muscles will be measured using electromyography (EMG). EMG involves attaching two electrodes (like stickers) to the skin over the muscles of the forearm and shoulder. Because of the location of these electrodes, it would be best to wear a short-sleeved shirt for the study. Before we put the electrodes on, we will clean your skin with a gentle exfoliating gel and an alcohol wipe.

Tracing task

The tracing task in this study will last about 35 minutes. The task involves using a touchscreen monitor on which you will be asked to imagine performing and physically perform the task. The task involves watching a white circle trace out a shape on the screen in different patterns, always beginning and ending at the same location. After the white circle disappears, a red circle will prompt you to begin. For trials that you are instructed to perform motor imagery, you will place and hold the index fingertip of your non-dominant hand on the red circle and imagine yourself re-creating the shape that was traced on the touch screen. After you are done imagining yourself re-creating the shape, you will lift your index fingertip off the red circle. For trials that you are instructed to physically perform motor imagery, you will use your dominant hand to touch the red circle and physically trace the shape that was traced on the touch screen.

During both the motor imagery and physical execution trials, we will be recording muscle activity from your dominant arm (i.e., the arm that you would naturally use to complete the physical execution of the task). You will be given breaks to make sure you don't tire.

Finger-tapping task

The finger-tapping task in this study will last about 35 minutes. The task involves using a keyboard on which you will perform the task. In this task, you will imagine yourself pressing a key on the keyboard that corresponds to an auditory cue. This auditory cue will consist of a male voice speaking the number of the key to be imagined. If you press a button during the training block, an error tone will play, and the error response will be recorded. Each individual key pressing event will last 1.5s and you will have a rest between each block. Immediately following the training blocks, you will perform this task physically. That is, you will perform the task by actually pressing the key corresponding to the auditory cue of the trial. Otherwise, everything that occurred during the previous trials will remain exactly the same. During the study, we will not be able to talk to you about your performance, but we will discuss your results with you after the study session.

During both of the tasks in the experiment, you will be seated comfortably in a chair with one hand resting on your lap and the other resting on a keyboard or the touch screen monitor, depending on which task you are performing at the time. You will be provided with 3 minutes of rest in between each block. During each trial, we will use transcranial magnetic stimulation (TMS) to measure your brain excitability, which is described in the next section.

Transcranial Magnetic Stimulation (TMS)

WHAT IS TMS?

A TMS machine uses electricity to create a magnetic field. TMS involves delivering brief magnetic pulses over different locations on your head. Basically, a TMS machine stores electricity, and then uses this electricity to make a magnetic field in a small coil that is held over your head. The magnetic field creates a flow of electrical current in your head. This current can evoke a small muscle twitch, when the pulse is delivered over the part of your head that corresponds to movement. No permanent changes to your brain will result from TMS.

TMS PROCEDURE

You will be comfortably seated in a chair with your hands resting on your lap. The TMS coil will be positioned on your head. During this time, you will be asked to sit quietly and keep your head as still as possible. During motor imagery blocks, you will hear a clicking noise as the current flows through the coil. When determining the position of the TMS coil, the pulses may cause your finger to move. You may also feel some tingling sensations on the head where the TMS coil is located. You will hear the same clicking noises as the current flows through the coil every two minutes during the imagery session.

During the study we will not be able to talk to you about your performance, but we will discuss your results with you after the study session. You will be provided with breaks to make sure you don't tire.

Possible Benefits, Risks and Discomforts

There are risks with this, or any study. We do not want to alarm you but we do want to make sure that if you decide to participate in the study, you have had a chance to think about the risks carefully. Please also be aware that there may be risks in participating in this study that we do not know about yet.

Potential Risks of TMS

TMS has been approved in Canada for both therapeutic and research use, and has been used in numerous studies worldwide since 1985. TMS has been shown to be extremely safe as long as proper safety precautions are taken. In general, the TMS procedure produces no pain and causes no known short-term or long-term damage of any kind. We will contact you if any new risks are discovered during the time of this study. Please contact us or ask your physician to contact us if you experience any effects that you feel may be a result of your participation in the study. TMS is painless, although it can cause tingling or twitching of muscles in the face, which may lead to soreness.

Common risks (1 or more out of every 100 people but less than 1 out of every 10 people have experienced the following):

- Headaches, which are caused by muscle tension. In the case of a headache, you will be advised to take whatever pain medication you usually take for mild headaches, which in most cases promptly resolves the discomfort.

- Neck stiffness and pain. This is believed to be due to the straight posture of the head and neck during the application rTMS, which involves a continuous train of pulses vs. single pulses delivered at a time as in the current study. In the case of such an event, you will be advised to take whatever pain medication you usually take for mild headaches, which in most cases promptly resolves the discomfort. You should advise a member of the research team at the first opportunity if you experience any neck stiffness or soreness. In this situation, you may opt to withdraw from the study or to rest and change posture for several minutes before the procedures are resumed.

Rare risks (1 or more out of every 10,000 people but less than 1 out of every 1000 people have experienced the following):

- In rare cases, seizures have been known to occur after TMS. However, the risk of seizure is *very low* except in people with epilepsy or people taking certain medications and is related to a type of TMS that involves a continuous train of pulses (vs. single pulses as employed in the current study). You will be asked to complete a TMS screening form, and precautions will be taken to ensure your safety such as removal of metallic objects from your body. Despite these precautions, TMS can induce a convulsion even in people who do not have brain lesions, epilepsy, or other risk factors for seizures. However, only 16 cases of convulsions induced by TMS in participants without risk factors for epilepsy have been reported despite the fact that many thousands of subjects have been studied worldwide. The overall risk for seizures during TMS is thought to be less than 1 in 1,000 patients. As with seizures in general, the seizures induced by TMS are usually brief and without serious physical consequences. The forms of magnetic stimulation that will be used during this study are well within the limits recommended by the safety guidelines.
- In the event a participant does experience a seizure, one of the two investigators will remain with the study participant at all times while the other contacts Dalhousie Security Services at extension 4109 to inform campus police of the location of the incident to facilitate the arrival of emergency personnel (Security Services coordinates with external emergency services and thus there is no requirement for lab personnel to contact 911).

TMS produces a loud clicking noise when the current passes through the handle of the machine. This loud click can result in ringing in the ears and temporary hearing problems

if no ear protection is used. To prevent this, you will wear earplugs which we will provide for you. Animal and human studies have shown that earplugs can effectively prevent the risk of hearing disturbances.

TMS is generally safe unless you have metal or magnetized objects in your body. Examples of these metal objects are cardiac pacemakers, surgical clips (e.g., aneurysm clips in your head), artificial heart valves, cochlear implants, metal fragments in your eyes, electronic stimulators, and implanted pumps. If you have any of these, you will not be able to participate in this study.

Potential Risks Associated With Behavioural Tasks

The risks associated with behavioural tasks are minimal; you may become bored or fatigued from participating in this research. However, you will be given breaks between imagery tasks to reduce these risks.

Potential Risks of Recording Muscle Activity (EMG)

There is minimal risk related to the use of this technique. The electrodes lie on top of the skin (like a sticker on your skin) and a conductive gel provides the contact between the skin and the electrodes. In uncommon instances (1 or more out of every 10,000 people but less than 1 out of every 1000 people) it is possible that your skin may be sensitive to the conductive gel, alcohol or adhesive used in the application of the electrodes. In such cases a rash or reddening of the skin is possible. This usually goes away in less than 24 hours.

Compensation / Reimbursement

You will be paid \$30, regardless of whether you complete the session or not. This compensation is intended as an honorarium — a gesture of appreciation for volunteering your time — and not as a form of employment or fee for service.

If you are participating in this study via the Dalhousie Undergraduate Psychology Pool (SONA) you will be given the equivalent number of SONA points (instead of the honorarium) up to the maximum approved by the Department of Psychology and Neuroscience. That is, you will be awarded 2.5 points for the single, 150-minute session. You will still receive your SONA points if you decide to stop participating in the study.

How your information will be protected:

Privacy: Protecting your privacy is an important part of this study. Every effort to protect your privacy will be made. No identifying information (such as your name) will be sent outside of Dalhousie University. If the results of this study are presented to the public, nobody will be able to tell that you were in the study.

If you decide to participate in this study, the research team will look at your personal information and collect only the information they need for this study, such as your;

- Age
- Biological sex
- Information from the study questionnaires

Confidentiality: In order to protect your privacy and keep your participation in the study confidential, you will be anonymized using a study code. For the purpose of data analyses, all participants will only be identified by their study code (e.g. s001). All hard copy data associated with the study (including this consent form) will be stored in a locked cabinet in a secured laboratory that is accessible only to lab personnel via personalized pin codes and who are trained in confidentiality. All data collected will be stored on a secure, password-protected server in the Laboratory for Brain Recovery and Function. No documentation will exist (hard copy or electronic) that links your name with your study code.

Data retention: Information that you provide to us will be kept private. Only the research team at Dalhousie University will have access to this information. We will describe and share our findings in theses, presentations, public media, journal articles, etc. We will be very careful to only talk about group results so that no one will be identified. This means that ***you will not be identified in any way in our reports***. The people who work with us have an obligation to keep all research information private. Also, we will use a participant number (not your name) in our written and computer records so that the information we have about you contains no names. All your identifying information will be securely stored. All electronic records will be kept secure, password protected server in the Laboratory for Brain Recovery and Function. In the event that a publisher requires study data to be a part of a public data repository (where data is stored and can be accessed by members of the public to improve transparency in science) only anonymized data is included meaning that you will not be identified in any way.

If You Decide to Stop Participating

You may choose not to continue your participation in the study at any time, (i.e. during the TMS portion or during the motor imagery tasks). If you decide not to take part in the study or if you leave the session early, your data will be automatically withdrawn from the study. Once you complete the session, your data can be withdrawn from the study upon request.

How to Obtain Results

If you would like a description of the results at the end of the study, you can obtain a short description of these results by visiting boelab.com in approximately 12 months. No individual results will be provided.

Questions

We are happy to talk with you about any questions or concerns you may have about your participation in this research study. For further information about the study you may call the principal investigator, who is the person in charge of this study.

The principal investigator is Dr. Shaun Boe.

Telephone: (902) 494-6360

We will also tell you if any new information comes up that could affect your decision to participate.

If you have any ethical concerns about your participation in this research, you may also contact Research Ethics, Dalhousie University at (902) 494-1462, or email: ethics@dal.ca (and reference REB file # 2022-XXXX).

Other

Neither the Principal Investigator nor any other individuals associated with the administration of this study have any financial interest in its outcome.

In the next part you will be asked if you agree (consent) to join this study. If the answer is “yes”, you will need to sign the form.

Signature Page

Project Title: Investigating the effect of task nature on corticospinal excitability during motor imagery

Co-Investigators:

Dr. S.G. Boe
Professor
School of Physiotherapy
Dalhousie University
(902) 494-6360
s.boe@dal.ca

H.J. Barr
MSc Candidate
Rehabilitation Research
Dalhousie University
hudson.barr@dal.ca

I have read the explanation about this study. I have been given the opportunity to discuss it and my questions have been answered to my satisfaction. I agree to take part in this study. My participation is voluntary and I understand that I am free to withdraw from the study at any time, prior to data analysis. I understand I will be given a copy of this consent form.

I agree to have my data included in a public research database Yes No

Name of Participant

Signature of Participant

Date

Name of Investigator

Signature of Investigator

Date

Appendix C: Motor Imagery Familiarization Script

Motor imagery is the mental performance of a movement – this means that you don't physically perform the movement. Instead you imagine yourself doing it by creating a picture of it in your head. There are two ways you can do motor imagery. The first is by picturing yourself performing the movement, and the second is by picturing someone else doing the movement. For this study we want you to imagine yourself doing the movement.

Doing motor imagery can be difficult at first, but there are a few things that can help you get better at it. One thing you can do is to try and relax – take a couple of slow, deep breaths and let yourself sink into the chair. As you are sitting there think about how the chair feels, and the position of your body. Another thing you can do is to think about how it feels when you actually perform the movement. How is your hand moving? How long does each movement take? All of these sensations can be used to make the picture in your head more vivid.

As we mentioned before there are two ways to do motor imagery. The first is by picturing yourself performing the movement and the second is by picturing someone else doing the movement. For this study we want you to imagine yourself doing the movement. You should be able to see your arm and hand, and your fingers moving up and down as you press each button, or your arm and hand move as you imagine yourself tracing on the screen. While you are imagining yourself doing the tasks, you can also think about how it feels when you're pressing each of the button or tracing on the screen.

Appendix D: KVIQ Questionnaire

Quantifying Imagined Movement in Non-Disabled and Pathological Systems

Participant Information			
Participant Code: _____	Group:	Date (dd/mm/yy): / /	
SCORING: KVIQ			
Movement	Visual	Kinesthetic	Comments
Forward shoulder flexion	/ 5	/ 5	
Thumb-fingers opposition	/ 5	/ 5	
Forward trunk flexion	/ 5	/ 5	
Hip abduction	/ 5	/ 5	
Foot tapping	/ 5	/ 5	
Total	/ 25	/ 25	

The Kinesthetic and Visual Imagery Questionnaire (KVIQ)											
	Movements	Visual					Kinesthetic				
1.	Forward shoulder flexion (nd)	1	2	3	4	5	1	2	3	4	5
2.	Thumb-fingers opposition (d)	1	2	3	4	5	1	2	3	4	5
3.	Forward trunk flexion	1	2	3	4	5	1	2	3	4	5
4.	Hip abduction (d)	1	2	3	4	5	1	2	3	4	5
5.	Foot tapping (nd)	1	2	3	4	5	1	2	3	4	5
Totals		/25					/25				

KVIQ Script:

This questionnaire assesses the clarity and intensity with which a person can perform motor imagery, which is the mental performance of a movement. The questionnaire involves performing and then imagining performing five different body movements. For each movement I will physically demonstrate how to perform it, and then ask you to perform it as well. After physically performing the movement, I'll ask you to mentally perform the movement two ways: imagining someone else performing the movement, or from the third person perspective (always done first); and imagining yourself performing the movement, or from the first person perspective. Some of these movements will be performed and imagined using the left side of your body, and others the right side of your body.

Just to remind you, imagining a movement from the third person perspective is you imagining someone else performing the movement. For example, imagining watching someone else shooting a basketball.

Imagining a movement from the first person perspective is you imagining yourself performing the movement. For example, imagining yourself shooting a basketball.

After each imagined movement, I will ask you to rate on a scale from 1 to 5 how clear the image was (third person perspective) associated with the imagined movement, and how intense (first person perspective) the sensations were.

*Here are the two scales that we will use to rate the imagined movements – **show/explain the two scales to the participant.***

Do you have any questions?

-- No

Let's begin. Here is the first movement.

- Demonstrate the "forward shoulder flexion" of the **Non-Dominant** hand
- Have them execute the movement

Good Job! Now we are going to imagine this movement visually. This again is to imagine the movement from a 3rd person perspective, as if you are watching someone else complete the movement.

- *On this scale, how intense was the imagined movement.* Show them the visual scale of clarity

Now we are going to imagine this movement kinesthetically. This again is to imagine the movement from a 1st person perspective, as if you are watching yourself complete the movement

- *On this scale, how clear was the imagined movement?* Show them the kinesthetic scale of intensity
 - ** Repeat the same process for the remaining four movements **

CLARITY – THIRD PERSON PERSPECTIVE

- 5 - Imagine as clear as seeing
- 4 - Clear image
- 3 - Moderately clear image
- 2 - Blurry image
- 1 - No image

INTENSITY – FIRST PERSON PERSPECTIVE

- 5 - As intense as executing the action
- 4 - Intense
- 3 - Moderately intense
- 2 - Mildly intense
- 1 - No sensation