INVESTIGATING THE EFFECT OF MANIPULATING EFFECTOR LOAD ON CORTICOSPINAL EXCITABILITY DURING MOTOR IMAGERY

by

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Abstract

Motor imagery drives motor skill improvement and acquisition, however recent research suggests the theories proposed to explain how this occurs may not fully account for the patterns of brain activation observed during imagery. This study probed the validity of imagery theories by comparing how corticospinal excitability scales during imagined and overtly executed performance of a grip task at varying forces. Participants completed 160 trials at 10-80% of their maximum voluntary contraction. Half the trials were performed via imagery, half via overt execution. Participants were pseudorandomized into high and low fidelity groups. A single pulse of TMS measured corticospinal excitability in each trial. Results showed that while corticospinal excitability increased across forces in imagery and overt execution, the trend was significantly different between modalities. There was no effect of image fidelity on corticospinal excitability. Results indicate that none of the current theories can fully explain the mechanisms involved in motor imagery.

List of Abbreviations Used

TMS – Transcranial Magnetic Stimulation

M1 – Primary Motor Cortex

EMG – Electromyography

MEP – Motor Evoked Potential

RMT – Resting Motor Threshold

FEM – Functional Equivalence Model

MST – Motor Simulation Theory

PFC – Prefrontal Cortex

PPC – Posterior Parietal Cortex

PMA – Premotor Area

SMA – Supplementary Motor Area

IPL – Inferior Parietal Lobule

MCM – Motor Cognitive Model

DLPFC – Dorsolateral Prefrontal Cortex

KVIQ – Kinesthetic Visual Imagery Questionnaire

MRI – Magnetic Resonance Imaging

FDS – Flexor Digitorum Superficialis

FDP – Flexor Digitorum Profundis

FPL – Flexor Pollicis Longus

APB – Abductor Pollicis Brevis

EDC – Extensor Digitorum Communis

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Chapter 1: Introduction

1.1 Motor Learning

Motor learning is the improvement or acquisition of motor skills resulting from practice. In a classic theory of motor skill acquisition proposed by Fitts & Posner (1967), motor performance is described as occurring in three stages: cognitive, associative, and autonomous. The cognitive stage is the first stage, representing the period during which the goals of the task are established, and explicit knowledge is used to determine the appropriate actions needed to achieve said goals. Subsequently, the associative stage involves focusing attention on specific aspects of the motor sequence, coordinating the execution of the movement. Finally, the autonomous stage is reached, in which performance of the action becomes an automatic process (Fitts & Posner, 1967). Since the publication of this theory, several other motor learning theories have been proposed building on this concept. In 1981 Newell & Rosenbloom proposed the power law function for motor learning based on the principle that skill learning is continuous, and this function became a strong feature of subsequent theories of motor learning (Shaw & Alley, 1985; Logan, 1988; Salmoni, 1989).

Though varying in the specifics of their psychological basis, in general most theories postulate that skill acquisition is a result of improved memory constructs of movement dynamics in relation to a specific task's demands (Fitts & Posner, 1967; Adams, 1971; Schmidt, 1975; Logan, 1988; Newell, 1991). Repeated exposure to a motor task offers the opportunity to receive feedback (sensory, environmental, etc.) about task performance allowing identification and correction of errors to refine the movement, reshape the internal representation of the action, and improve performance (Newell, 1991). These theories align with the neurophysiological properties of plasticity; practice

of a motor skill drives activity-dependent changes in synaptic connectivity, strengthening the neural networks involved in coordinating the practiced movement (Johnston, 2009). Repetitive stimulation of synapses drives long-term potentiation and depression, which are characterized by physical changes in dendritic spines and neuronal circuits (Johnston, 2009). These long-term changes in neural connectivity are the basis of learning (Xu et. al., 2009; Yang et. al., 2009; Caroni et. al., 2012).

1.2 Motor Imagery

Given the neurophysiological changes that are associated with physical practice of a motor skill, it is unsurprising that this is the gold standard method of motor learning. There are, however, alternative methods of practicing motor skills that do not involve physical execution and have been proven to facilitate neural plasticity and promote motor learning (Jeannerod, 1995; Pascual-Leone et. al., 1995; Mizuguchi & Kanosue, 2017). One of the most employed alternatives to physical practice is motor imagery, the mental rehearsal of a motor task in the absence of overt movement (Decety & Grezes, 1999). Practice via motor imagery can be used as a method of driving motor learning in both the cases of rehabilitation following brain injury (Page et al., 2001; Ang et al., 2015), and in competitive sports training (Guillot & Collet, 2008; Afrouzeh et al., 2015), and some evidence suggests mental practice may hold merit as an occupational training tool, particularly in the medical field (Sanders et. al., 2008; Schuster et. al., 2011).

The reason motor imagery is considered a useful approach to motor learning in these instances is its similarity to overt movement, demonstrated in a broad body of literature showing there are numerous brain regions that exhibit similar patterns of activation during both imagined and overt performance of motor tasks (Decety & Grezes,

1999; Jeannerod, 2001; Kraeutner et al., 2014). Consequently, mental practice of a motor task is thought to be capable of driving synaptic changes in the brain much like those that occur during physically practiced tasks (Driskell et. al., 1994; Munzert & Zentgraf, 2009; Ruffino et. al., 2017), promoting learning. Many studies have shown that corticospinal excitability is increased during motor imagery performance in comparison to rest (Rossi et. al., 1998; Hashimoto & Rothwell, 1999; Stinear & Byblow, 2004; Meers et. al., 2020; Lee et. al., 2020), providing empirical evidence that this modality at the very least increases the potential for motor learning to occur by increasing neuronal excitability. Benefits have been observed in motor performance when imagery is used as an adjunct to physical practice (Holmes & Collins, 2001; Page et. al., 2007; Schuster et. al., 2011; Kraeutner et. al., 2014), and an increasing amount of evidence supports motor imagery as an alternative therapy on its own in instances when physical execution of motor tasks is severely impaired or impossible, such as in the case of stroke (Sharma, 2006; Ertelt et. al., 2007; Gowda et. al., 2021).

1.3 Theories of Motor Imagery

Research on motor imagery has yielded multiple theories to explain how imagined practice of a motor task can improve physical performance (e.g., Decety & Grezes, 2001; Jeannerod, 2001; Grush, 2004; Glover & Baran, 2017), however, there is yet to be proposed a theory that fully accounts for the mechanisms underlying motor imagery, and it is not completely understood how exactly this modality works to promote motor learning. The notion of a functional equivalence between imagined and overt movement has predominated the literature in the domains of both fundamental and applied research and consequently, prescription of imagery-based therapies and motor

learning paradigms are largely based on the parallels between these modalities. A recently published review (Gaughan & Boe, 2021) however, highlights the lack of a dose-response relationship for imagery-based therapies in survivors of stroke. While there is a clearly defined pattern between dosage of physical therapy and outcomes for motor function (Lang et. al., 2015), the dosage of prescribed imagery-based therapies is variable across studies and has no clear relationship with functional outcomes. This evidence suggests that employing imagery-based therapies and motor learning paradigms based on the premise that they are equivalent to overt movement may not be utilizing this modality as effectively as possible.

For motor imagery to be used effectively as a tool for motor learning, it is paramount to understand the neural mechanisms underlying imagery practice and the parameters with which to apply imagery-based learning paradigms to optimize motor outcomes. One concept starting to emerge in contemporary theories of motor imagery is that of image fidelity. Image fidelity refers to how familiar one is with the components involved in executing a given movement, which in turn influences how accurately they can create a representation of that movement via imagery (Jeannerod, 1997; 2001; Slifkin et. al., 2008; Glover & Baran, 2017). If skill acquisition via imagined performance is – like that which occurs via overt execution – a result of improved memory constructs of movement dynamics in relation to a specific task's demands, then the ability to produce high fidelity imagery may be a determining factor in learning via this modality. Few studies have explored the potential role of image fidelity in learning via motor imagery.

There is currently conflicting evidence as to whether brain activity during tasks imagined at varying efforts mirrors that of tasks performed overtly at varying efforts.

Studies that have explored the relationship between effort and brain activity during overt movement have found that as the effort required to complete a task increases, brain activity increases as well (Dai et al., 2001; van Duinen et al., 2008; Perez & Cohen, 2009; Park & Li, 2013). According to predominant theories of motor imagery that purport a functional equivalence between imagined and overt movement, brain activity should scale with effort in a similar way when this type of task is performed via imagery.

Some research has confirmed that this holds true in imagery tasks that manipulate effort; for instance, one study found that duration of arm movements at different loads (0, 1 and 1.5kg) scaled similarly for both imagined and executed movements (Papaxanthis et. al., 2002). Other studies comparing imagined and overt movement of actions at varying degrees of effort have obtained similar results (Gentili et. al., 2004; Mizugushi et. al., 2013; Helm et. al., 2015). However, results of comparable studies in the field suggest that functional differences are occurring when effort is manipulated in imagined compared to overt movement. For example, one study found that while there was no difference in the time it took participants to imagine walking a certain distance (5, 10 or 15 m) compared to actual walking, when participants put on a 25kg backpack and were asked to perform the same task, duration of the imagined movement increased significantly, while duration of the executed movement stayed the same (Decety et. al., 1989). There are other studies that have found similar differences between imagined and overt movements when effort is manipulated (Park & Li, 2011; Cerritelli et. al., 2000; Slifkin et. al., 2008). One possible explanation for the divide in the literature is that several of these studies fail to provide a definition of what exactly "effort" is and rely primarily on behavioural measures such as self-reported movement duration.

Owing to the conflicting evidence as to whether brain activity during tasks imagined at varying efforts mirrors that of tasks physically performed at varying efforts, the primary objective of this study is to compare brain activity (assessed via corticospinal excitability) during imagined performance of a grip task at varying forces to corticospinal excitability during overt performance of the same task. This comparison will offer evidence towards the theoretical framework of motor imagery, namely informing on theories built on the concept of functional equivalence. Given the previous research in this domain, it was hypothesized that during overt performance of the task, corticospinal excitability will demonstrate a positive, linear relationship with force. Based on existing evidence that summarizes brain activity during imagined performance, it was hypothesized that corticospinal excitability will demonstrate a similar positive, linear trend at low forces but plateau as force is increased.

The secondary objective of this study is to explore the role of image fidelity in learning via imagery. To accomplish this, the study employed a task requiring participants to accurately achieve varying levels of force (relative to their maximum voluntary contraction) with concurrent assessment of corticospinal excitability during either imagined or overt movement. A high (overt movement followed by imagined) and low (imagined movement followed by overt) fidelity version of the task was used to compare whether image fidelity influences corticospinal excitability during imagined task performance. Given that motor learning models emphasize the need for repeated exposure to a task to strengthen synaptic connections and improve the memory constructs of a given movement's dynamics, familiarity with a task should allow for higher fidelity imagery, enriching the experienced image and leading to increased activation of the

motor system. Thus, it was hypothesized that a high-fidelity group would demonstrate increased corticospinal excitability during imagery performance compared to a low-fidelity group.

Chapter 2: Background & Rationale

2.1 Stroke & Neurorehabilitation

The main goal of physical rehabilitation post-stroke is to increase activity within the affected brain regions to maintain and restore neural connections that may otherwise be lost over time (Coleman et. al., 2017). Maintaining the neural networks involved in motor function promotes motor learning and increases an individual's chances for improved functionality as they progress through their recovery (Krakauer, 2006). Because motor imagery is known to activate many similar brain regions as are active during overt movement, it is used as an adjunct (Page et. al., 2007; Schuster et. al., 2011) or alternative (Erltelt et. al., 2007; Gowda et. al., 2021) to traditional physical therapy. Systematic reviews exploring the effects of imagery practice on stroke rehabilitation, however, have been inconclusive in determining whether imagery-based therapies offer beneficial effects.

In a 2015 review of 10 studies that had used motor imagery as an adjunct therapy with physical rehabilitation, the authors found there were no differences in recovery between patients who received motor imagery therapy and those who did not and concluded that imagery is not an effective means of improving upper limb function following stroke (Machado et. al., 2015). More recently, a Cochrane review of 25 studies concluded that motor imagery in addition to other therapies was more beneficial in improving upper limb function, however, a further analysis of 3 studies comparing motor imagery versus conventional physical therapy provided low-certainty evidence that imagery alone may not improve upper extremity impairments (Barclay et. al., 2020). Overall, the evidence towards motor imagery as a therapeutic tool for neurorehabilitation

is inconsistent, and more research is needed to determine how best to utilize imagery as a motor learning tool.

2.2 Transcranial Magnetic Stimulation

It has been well-established that during motor imagery performance, corticospinal excitability is increased in comparison to during rest (Rossi et. al., 1998; Hashimoto & Rothwell, 1999; Stinear & Byblow, 2003; Meers et. al., 2020). Knowing this, much of the research on motor imagery has employed the use of transcranial magnetic stimulation (TMS) to measure corticospinal excitability during imagery sessions. Transcranial magnetic stimulation is a neurostimulation and neuromodulation technique that operates based on the principles of electromagnetic induction of an electrical field in the brain. This field can allow for electrical current to pass through the skull and depolarize neurons, either decreasing or increasing cortical excitability (Rossi et. al., 2009). This form of stimulation can be delivered with high precision to a specific brain area (Hallet, 2000). In targeting the primary motor cortex (M1), neurons that give rise to the corticospinal tract can be stimulated resulting in depolarization and ultimately the activation of a target muscle, which results in an observable and quantifiable motor response (Hallet, 2000; Rossini et. al., 1994).

When stimulating the motor cortex, pyramidal neurons of the corticospinal tract become depolarized. The recruitment of corticospinal neurons is thought to occur indirectly via horizontal connections, rather than directly via the induced current (Rothwell, 2005). The corticospinal tract is primarily responsible for voluntary motor activity, controlling top-down initiated movements in the somatic motor system (Rothwell, 2005). Electromyography (EMG) overlying the muscle of interest can be used

to obtain the motor evoked potentials (MEPs) that occur because of stimulation and muscle activation (described in detail below). Transcranial magnetic stimulation is often used in assessments and manipulations of M1, as this area of the brain is not only easily accessible for stimulation, but responses can be quantified based on the evoked muscle response (Hallet, 2000).

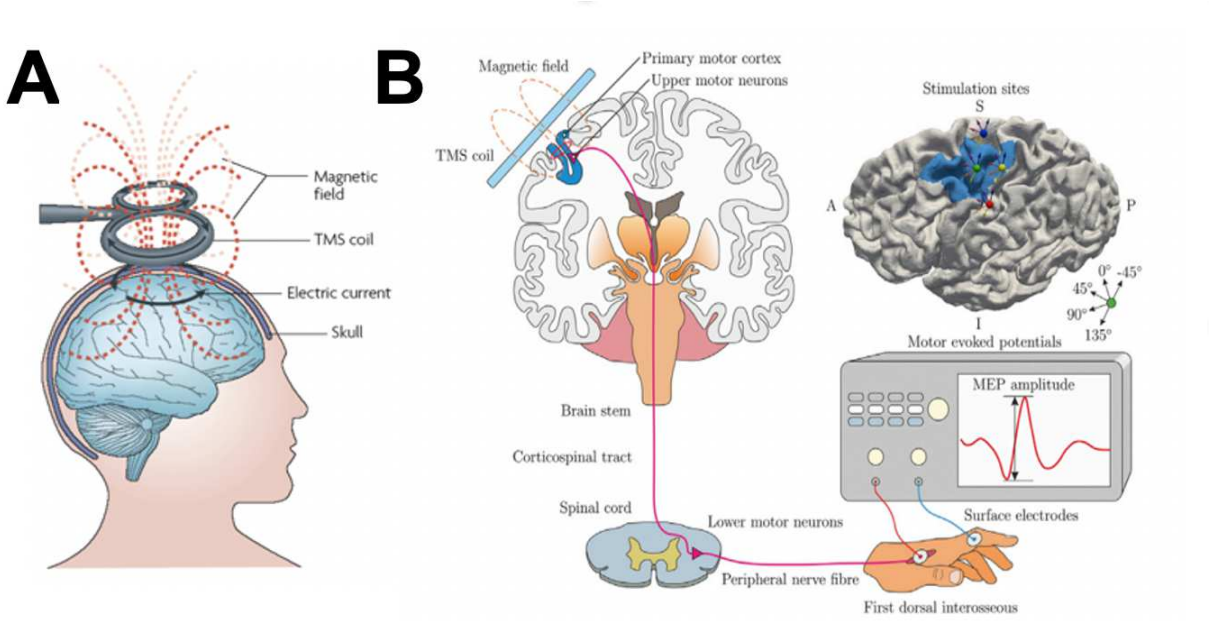

Figure 1. Application of TMS & Measurement of MEPs. (A) A TMS coil is shown positioned over the skull, with the generated magnetic field and electrical current depicted (Spronk et. al., 2011). (B) A diagram depicting the neurophysiological response to TMS stimulation. Electrical stimulation on the surface of the skull depolarizes neurons in the corticospinal tract, resulting in a response in the target muscle that produces an MEP (Weise et. al., 2019).

2.2.1 Corticospinal Excitability

The strength of the response of corticospinal neurons to a given stimulation is quantified as corticospinal excitability (Rothwell, 2005). In TMS studies, a baseline level of corticospinal excitability, called the resting motor threshold (RMT) is determined as the lowest level of stimulation which will reliably elicit a muscle response (Borckardt et.

al., 2006). Once established, RMT can be used in experimental designs to determine the effect of a manipulation on corticospinal excitability. Corticospinal excitability is quantified by changes in MEP amplitude and is reflective of changes in neuronal excitability at either the cortical level, spinal level, or both (Rothwell, 2005).

2.2.2 Resting Motor Threshold (RMT)

Resting motor threshold is defined as the minimal stimulation intensity at which the target muscle produces an MEP with amplitude ≥ 50 μV in at least 50% of trials (Borckardt et. al., 2006). Establishing RMT is of critical importance in TMS studies. Trial-to-trial variability in MEP amplitude often occurs due to intrinsic changes in the excitability of cortical and spinal neurons (Rossini et. al., 2015). This physiological noise causes some uncertainty when measuring RMT, however controllable factors such as coil position, background EMG activity, participant position, time of day, environmental noise, and participant's arousal level can and should be kept constant to improve reliability of the measure (Rossini et. al., 2015). It has been shown that within individuals, RMT values increase when measured following use of drugs that have an excitatory effect on the brain (Rossini et. al., 2015) and following physical activity (Ah Sen et. al., 2017), indicating that when extrinsic and intrinsic factors are kept constant, RMT is a reliable within-individual measure of base-level corticospinal excitability (it should be noted that due to the nature of the measure, RMT cannot directly be compared between individuals, however mean MEP amplitude can be as it is a standardized measure (Rossini et. al., 2015)).

2.2.3 Motor Evoked Potentials (MEPs)

Motor evoked potentials are the electrical signals recorded from the muscle via EMG following stimulation (see Figure 1B). The most important characteristics of the MEP are i) amplitude, which represents the strength of the motor response, and ii) latency, which indicates the conduction time of the propagating action potential (Rossini et. al., 2015). MEP amplitude is subject to changes from both intrinsic (such as mental activity) and extrinsic (such as environmental stimuli) factors. The former are difficult to control and therefore introduce variability in amplitude of MEPs collected either when determining RMT or during experimental trials. To reduce the effects of intrinsic factors, many MEPs should be collected, and the mean MEP amplitude over numerous trials should be used when analyzing MEP data (Rossini et. al., 2015). MEP latency is of particular importance when TMS is diagnostic in nature because slower nerve conduction is indicative of demyelinating conditions (Kallioniemi et. al., 2015), however MEP latency should be checked in healthy subjects to confirm that the latency is of a normal timeframe.

2.2.4 Single Pulse TMS

There are multiple methods of applying stimulation depending on the desired outcome. Single pulse, paired pulse, and repetitive stimulation are the three types of TMS. Paired pulse stimulation involves the administration of two stimuli delivered within milliseconds of one another, while repetitive TMS involves rapid delivery of a train of stimuli. The current study focuses on single pulse TMS; readers are referred elsewhere for more information on alternate forms of TMS (see Rossini et. al., 2015). Single pulse TMS involves single stimuli, typically delivered at threshold or suprathreshold level

(Rossini et. al., 2015). Single pulse TMS has high spatial and temporal resolution (Hallet, 2007; Bolognini & Ro, 2010) and is a reliable tool for measuring corticospinal excitability in upper-limb musculature (Plowman-Prine et. al., 2008). Stimuli must be delivered with a minimum interstimulus interval of 3 sec to ensure that corticospinal neurons return to their resting state between delivery of stimuli, so that the observed effects are a direct result of the stimulation (Rossini et. al., 2015).

2.3 Motor Simulation Theory & the Functional Equivalence Model

As discussed, the application of imagery-based therapies as a motor learning tool is centered largely on the premise that similar patterns of brain activation occur during motor imagery as during overt movement, including that of regions identified as being 'motoric' in nature (Decety & Grezes, 1999; Jeannerod, 2001; Kraeutner et al., 2014). In their well-known meta-analysis conducted in 2000, Decety & Grezes compiled 30 neuroimaging studies whose tasks fell into one of four categories: execution, simulation, observation, or verbalization. After conducting analyses on the shared activations in functional anatomy during tasks performed via each of these modalities, the authors concluded that the activation of several common sites observed in action execution, simulation and observation favored a model of functional equivalence between these processes (Functional Equivalence Model; FEM). Near the same time, Jeannerod (2001) published a paper proposing the Motor Simulation Theory (MST), based on the concept of covert and overt stages of actions, that was similarly reliant on the idea of functional equivalence between imagined and overt movement.

The covert stage is best described as a planning stage, during which the movement one is about to perform is mentally represented. The representation includes

the goals of the action, the means of accomplishing it, and potential consequences of its performance, all of which are generated in the absence of external environmental cues (Jeannerod, 1994, 2001). The overt stage involves the physical execution of the action. Overt actions are monitored and adjusted with real-time sensory feedback (e.g., visual and proprioceptive; Paulignan et. al., 1991; Glover 2004; Cameron et. al., 2009), while covert actions are based on stored motor representations of the action (Jeannerod, 1997; Slifkin et. al., 2008; Glover & Baran, 2017). The covert and overt stages of action represent a continuum, whereby for an action to reach the overt stage, it must first go through the covert, or planning stage. On the other hand, covert actions can be performed without their overt counterparts, because the covert stage precedes the overt one (Jeannerod, 1994, 2001).

On this premise, Jeannerod argued that covert actions are identical to the planning stage of overt actions, and therefore share a neural similarity with the state where an action is simulated during execution, i.e., performance of a covert action simulates the brain activity observed during the same, executed action. This similarity allows for off-line rehearsal of motor tasks via a simulation mechanism that allows one to anticipate the performed action and its potential outcomes (Jeannerod, 2001, 2006). On a surface level, the mechanisms proposed in MST offered exciting new insight into the parallels observed between imagined and overt movements, and indeed much research has supported the idea of functional equivalence between these two modalities (Munzert & Zentgraf, 2009; Hetu et. al., 2013; Munzert et. al., 2015).

There is compelling evidence suggesting that neural similarities exist between overt and imagined actions. Multiple neuroimaging studies have shown that many of the

neuroanatomical regions activated during overt execution, including the prefrontal cortex (PFC), posterior parietal cortex (PPC), M1, pre-motor area (PMA), supplementary motor area (SMA), cerebellum and basal ganglia are also activated during imagery (Decety & Grezes, 2001; Hetu et. al., 2013; Hardwick et. al., 2018). It should be noted however that there is some discrepancy between research; for example, several early studies did not find consistent activation of M1 during imagery (Roland et. al., 1980; Decety et. al., 1988; Lozte et. al., 1999), however many subsequent studies showed significant activation of M1 during imagery performance (Decety & Grezes, 2001; Hetu et. al., 2013; Hardwick et. al., 2018). These conflicting observations may be because motor imagery demonstrates overall weaker neural activity than overt movement, a trend seen in both neuroimaging and connectivity studies, which may be demonstrative of inhibitory processes occurring during imagined movements to prevent action execution (Guillot et. al., 2012; Solomon et. al., 2019), a key postulate of MST (Jeannerod, 2001; 2006).

In addition to the neuroanatomical and neurophysiological similarities that are shared between imagined and overt movement, many studies have also shown that physiological measures such as respiratory rates, skin resistance, cardiovascular activity, EMG, etc. are highly correlated during imagined and overt actions (Decety et. al., 1991; Guillot et. al., 2007; Papadelis et. al., 2007; Collet & Guillot, 2011). In 1991 Decety et. al. demonstrated that during a motor imagery task that involved running on a treadmill at escalating speeds, cardiovascular and respiratory rates increased proportionally, as observed during overt movement. There is even some evidence to suggest that imagery performance is capable of increasing EMG activity in the absence of movement (Guillot et. al., 2007).

It has also been demonstrated that interruption or damage to parts of the motor system impair both imagined and overt movement similarly. For example, Parkinson's disease is a neurodegenerative disorder affecting dopaminergic neurons in the substantia nigra that leads to impaired movement (Dickson, 2018). Parkinson's disease can lead to slowed execution of movements, and those living with Parkinson's disease also demonstrate increased duration of imagined movements (Helmich et al., 2007; Heremans et al., 2011), indicating that on a neural level the impairments associated with Parkinson's disease in motor control centers of the brain similarly impact imagined and overt movement performance. Additionally, lesions to the parietal lobe and inhibition of the inferior parietal lobule (IPL) via TMS, a region of the parietal cortex thought to be involved in motor processes such as movement selection and planning (Rushworth et al., 2001; 2003), has been shown to impair the ability to perform motor imagery and acquire imagery-based skills (Sirigu et. al., 1996; Lebon et. al., 2012; McInnes et. al., 2016; Kraeutner et. al., 2016), as well as impairing the coordination of physical movements (McInnis et. al., 2016).

While there is no lack of support for a model based on functional equivalence, several postulates of MST are vague and have remained unspecified over time, and the evidence for MST and the FEM is not unequivocal. Jeannerod proposed that motor imagery involves "neural mechanisms similar to those operating during the real action", yet these mechanisms remain to be fully explained even though two decades have passed since the genesis of this theory. In 2017 O'Shea & Moran published a critical review of MST and the evidence supporting it to date. Their robust summary concluded that the processes of imagined and overt movement share several neural, neuropsychological, and

behavioural properties, and presented a myriad of evidence for several of the postulates of MST, including that the simulation process during motor imagery functions to i) assemble action elements stored in long-term memory, ii) monitor simulation of the action towards a goal, and iii) inhibit the overt movement. While they noted that the exact mechanism of simulation that MST is reliant on is ill-defined, their review highlighted the numerous regional activations shared between imagined and overt movements and supported the notion that a high degree of functional similarity exists between these two modalities (O'Shea & Moran, 2017).

2.4 Motor Cognitive Model

Despite the wide acceptance of the FEM and MST, some researchers remain dissatisfied with the incomplete evidence supporting these theories. In 2017 Glover & Baran proposed a different theory to explain the neural correlates between motor imagery, action observation and overt movement. The Motor-Cognitive Model (MCM) argues that the process of motor imagery involves central-executive functions that are not evident during overt movement. It is well established that overt movement is a two-stage process that involves both the planning and execution of a movement (Woodworth, 1899; Elliot et. al., 2001). The MCM proposes that as in overt actions, motor imagery – a covert action – is a two-stage process during which the components of planning are based on stored motor representations. This means that the planning stage is functionally similar for imagined and overt movements (Glover & Baran, 2017). However, during "execution", actions performed via imagery rely on conscious executive control, monitoring the image as it unfolds and elaborating it in real time. Conversely, because physically executed actions may be influenced by external factors, they access automatic

visual and proprioceptive feedback to monitor and fine-tune the movement in real time and rely on unconscious online control (Glover & Baran, 2017).

Because the MCM postulates that conscious control must be used to monitor the unfolding image, during imagined movements attention must be switched between the motor image and the action that is being simulated. During imagined performance of a well-known, simple action diverting attentional processes may be easy, however, complex or novel actions require more control, and this leads to differences between imagined and overt movements (Glover & Baran, 2017). While the FEM and MST explain only the similarities between imagined and overt movement, the MCM purports to explain both the similarities and the differences between the two, and consequently this model has been gaining traction in motor imagery literature (Glover & Baran, 2017; Glover et. al., 2020; Van der Lubbe et. al., 2021).

Glover and colleagues (2020) followed up their initial proposal of the MCM with a series of three experiments that used mental chronometry (the duration of imagined movements) to compare imagined vs. executed performance of a high precision grasping and placing motor task (Marteniuk et. al., 1987; Glover & Baran, 2017). In their second experiment, they implemented a high load manipulation to compare a simple version of the task to a more complex one and found that duration of imagined movements was more greatly impacted at high compared to low loads, offering further behavioral support for the MCM (Glover et. al., 2020). A review of several imagery studies conducted previously found that during imagined performance of complex motor skills there was consistent overestimation of the actual duration of time required to perform the motor

task (Guillot & Collet, 2005), showing that years of behavioural evidence supports the MCM theory.

A recently published electroencephalography (EEG) study employed the use of a discrete sequence production paradigm to explore changes in the synchronization of theta, alpha and beta band activity during imagined and overt movements (Van der Lubbe et. al., 2021). Arguably this task falls in the realm of complex tasks, which as predicted by the MCM should result in observed differences between imagined and overt execution. Indeed, the authors found that theta band activity was increased during imagery in comparison to overt movements, and that sensorimotor areas and regions associated with visuospatial attention were more active during overt execution than during imagery (Van der Lubbe et. al., 2021). In summary these findings offered more support for the MCM than for models based on functional equivalence.

While there is intriguing evidence towards the MCM and this framework offers the theoretical benefits of explaining the neural differences observed between imagined and overt movements that are not accounted for in MST or the FEM, the model is new and remains relatively unexplored and unsubstantiated in the current motor imagery literature. To date, only one study has moved beyond the behavioral manifestations of changes in brain activity to show that functional differences are occurring on a neural level in a manner that aligns with the hypotheses of the MCM. Though it may be theoretically favorable over MST and the FEM, the MCM is lacking in empirical support and requires further exploration to establish itself as a contending motor imagery model.

2.5 Other Models

MST and the FEM are by far the most widely recognized models proposed to explain the neural mechanisms of motor imagery. The MCM is relatively new and continues to be explored in the literature as a potentially promising model (Glover et. al., 2020; Van der Lubbe et. al., 2021). There are, however, other models that although less frequently cited in imagery literature have merit in their own rights and must be discussed and evaluated to thoroughly dissect the theoretical underpinnings of motor imagery.

2.5.1 Internal Models

In a simple feedforward control system, a set of muscle activations that drive an action towards a goal are defined prior to the onset of movement; after movement onset, the motor command unfolds unchanged until the movement is completed (Desmurget & Grafton, 2000). In a feedback system, the current state of the motor system is compared to a reference value, and when a discrepancy is detected between the current and reference states, an error signal is generated and the motor behavior is modulated (Desmurget & Grafton, 2000; Flanagan et. al., 1993). During motor execution in the real world, however, both internal and external factors play a huge role in motor processes, and the simple mechanisms of feedforward and feedback control cannot fully explain the neural processes involved in the modulation of actions (Desmurget & Grafton, 2000).

Internal models have been proposed to describe the neural mechanisms that are involved in mimicking the input/output characteristics (or their inverses) of actions (Kawato, 1999). Internal models are based on the concept that feedback mechanisms are used to modulate motor commands and guide actions towards a desired goal (Desmurget & Grafton, 2000). While some models, such as those favoring feedforward or feedback

control, postulate that action adjustments are modulated by sensory (based on sensory information) or non-sensory (based on efferent information) feedback, internal models argue that feedback is provided internally via both efferent and afferent signals (Desmurget & Grafton, 2000). Internal models can be further broken down into forward and inverse models.

Previous theoretical work in the realm of motor imagery has minimally (if at all) incorporated internal models, presumably because these models focus on motor control as opposed to imagery. More recently, however, internal models have begun to be taken into consideration as a potential component of imagery theories such as MST or emulation theory (described below) because of their ability to explain the mechanisms that occur during imagery (Kilteni et. al., 2018).

2.5.1.1 The Forward Model

In the context of motor control, prediction refers to estimating the future state of the motor system (Wolpert & Flanagan, 2001). While some motor commands may be perfunctory and simple, the human motor system must also be capable of predicting the consequences of motor commands in complex situations. The forward model has been proposed as a system that can simulate the dynamic nature of the body and environment, explained via a forward relationship between actions and their consequences (Wolpert & Flanagan, 2001).

In the most basic terms, the forward model mimics the causal flow of an action by predicting its next state given the current state and the motor command (Wolpert et. al., 1995). There are several aspects of the forward model that make it favourable from a theoretical perspective. Firstly, feedback mechanisms reliant on sensory information do

not consider that sensorimotor loops are large and feedback control via these pathways is too slow for rapid movements (Paillard, 1996; Desmurget & Grafton, 2000). Because the forward model is reliant on internal feedback, the outcome of an action can be estimated and used before sensory information has been processed and becomes available (Gerdes & Happee, 1994; Desmurget & Grafton, 2000). The forward model is also consistent with theories that hypothesize the motor system uses an efferent copy of motor commands to anticipate and modulate the sensory effects of movement (e.g., the MCM; Glover & Baran, 2017, and emulation theory; Grush, 2004), and can therefore be used for estimation in which the prediction of the next state is combined with a sensory-based correction (Desmurget & Grafton, 2000).

Skilled motor behaviour is reliant on the ability to generate accurate predictive models (Wolpert et. al., 1995). Due to the dynamic nature of the human body and the development of the motor system over time, it is imperative to both update existing models and acquire new ones. Forward models are not fixed but can be learned and altered through experience (Wolpert et. al., 1995). Another theoretical benefit of forward models is that they compare the predicted outcome to the actual outcome of a motor command, and use errors in prediction to update the model, improving future predictions. Thus, a forward model could be used to transform errors and provide signals for motor learning (Wolpert et. al., 1995). Similarly, the forward model could be implemented via simulation to predict the outcomes of actions in the absence of physical movement and promote motor learning via imagery (Jordan & Rumelhart, 1992; Wolpert et. al., 1995). There are many theoretical benefits of forward models, and recent research has

demonstrated evidence to support the existence of an internal forward model in the central nervous system during imagined movements (Kilteni et. al., 2018).

2.5.1.2 The Inverse Model

As with the forward model, feedback mechanisms reliant on sensory information cannot account for fast, coordinated movements as control via these pathways is too slow. Thus, the inverse model proposes that to execute control in a feedforward direction, the brain must first establish an inverse model of the dynamics of the movement via motor learning (Kawato, 1999). An inverse model considers the properties of the involved muscles and estimates the motor command that will result in the motor goal, however the model does not implement a motor plan prior to onset of the movement, instead continually monitoring the current state and comparing to the goal state, adjusting as needed (Wolpert et. al., 1995; Desmurget & Grafton, 2000; Grush, 2004).

There is some debate around the nature of the interaction between feedback systems and the motor system during movement. Some research favours forward models, some inverse models, and some propose that a combination of both types of modelling are involved in motor control (Flanagan et. al., 1993; Wolpert et. al., 1998; Desmurget et. al., 1999; Desmurget & Grafton, 2000). The theoretical arguments for forward models seem to outweigh those for the inverse model, and forward models are consistent with research that has demonstrated that learning can occur via motor imagery.

2.5.2 Emulation Theory

First developed by Richard Grush in 2004, the emulation theory of representation attempts to explain not only the processes of motor control and motor imagery, but also visual imagery and visual perception. Building on the forward model, emulation theory

proposes that during action implementation, a continuous stream of feedback is provided based on the dynamics of the musculoskeletal system. When performing an action, an individual will send "control signals" to the body, and the output of these signals is to monitor or adjust the movement to align with the goal. The concept unique to this theory is that when a control signal is sent by the individual, an efferent copy of the signal is simultaneously sent to a subsystem (the emulator) that implements the same input/output functions. For example, if the control signal informed an individual that their balance was off, the same input would be sent to the emulator, which would then provide the same output as the body, i.e., make postural changes to correct your balance (Grush, 2004).

In the context of imagined movements emulation theory purports that during motor imagery, the brain constructs visual models of both the body and the environment, and these models either create or direct efferent copies of inputs (i.e., control signals) to provide expected or predicted outputs in the absence of sensory feedback. Furthermore, these models can be stored for later representations of the image or the creation of new motor images, and even to predict the results of different actions or build new motor representations (Cuenca-Martinez et. al., 2020). Visual imagery and perception come into play in this ability to store and manipulate models. Emulation theory suggests that action observation facilitates the process of motor imagery because it provides the visual input between the body and the environment (Grush, 2004; Cuenca-Martinez et. al., 2020). This hypothesis is supported by many studies that have shown motor learning is better promoted by a combination of imagery and observation together simultaneously than by observation alone (Eaves et. al., 2016; Romano-Smith et. al., 2018; Meers et. al., 2020).

Emulation theory also proposes a mechanism by which deviations from optimal performance can occur via motor imagery. Recent research has begun to explore the idea that errors may be simulated during imagined performance, similarly to how they occur inherently during physical execution (O'Shea & Moran, 2017; Dahm & Rieger, 2019). During overt movement, detection of errors can occur based on three distinct comparison mechanisms: comparison of the intended action consequences to those of the performed action, comparison of the predicted action consequences to those of the performed action, or comparison of the intended action consequences to the predicted action consequences (Blakemore et al., 2002). During imagined movement there are no real consequences because the action is not actually performed, however if forward models predict action consequences, it may be possible to compare intended action consequences to predicted action consequences, providing the ability to detect errors even in the absence of physical execution (Grush, 2004; Dahm & Rieger, 2019). This framework is in line with the theoretical assumptions of MST and the FEM, in which imagined movements are considered a complete simulation of the action (Grush, 2004; Iachini, 2011; Jeannerod, 2001).

2.5.3 Embodiment Theories

Embodied cognition refers to several theories in a variety of areas within cognitive science (artificial intelligence, psychology, cognitive neuroscience, philosophy, linguistics, etc.). The embodied cognition approach to simulation contains many different views, with some authors emphasizing the role of the body in cognition, and others highlighting more generally the role of cognition during simulated states. In the context of motor imagery, some view simulation as a conscious process that involves the

deliberate rehearsal of previously performed actions (Decety & Ingvar, 1990; Munzert & Zentgraf, 2009). Jeannerod (2001) considered simulation as a covert process that involves the same neural networks as physical performance of actions. Others consider simulation as a form of re-enactment, during which the brain reactivates stored, multimodal representations and simulates the action, perception and introspection associated with it (Barsalou, 2008).

Embodiment theories encapsulate two distinct notions of simulation: on one hand, simulation is seen as a form of prediction that may be used to plan an action and understand its goals (Gallese, 2009; Borghi & Cimatti, 2010). On the other hand, simulation may be considered separate from prediction, instead utilized as a means of re-enacting or enhancing past sensorimotor experiences (Barsalou, 1999; Borghi & Cimatti, 2010). With respect to the latter account, simulation mechanisms are present across a spectrum of cognitive processes, suggesting that simulation is an independent process and plays an important computational role in the brain (Borghi & Cimatti, 2010). While some forms of simulation may occur unconsciously, motor imagery results from deliberate construction of action representations in working memory, drawing on interactions between the action, perception, the environment, and the body; in other words, imagined movements constitute an embodied simulation process (Barsalou, 2008).

In general, the theory of embodied cognition summarizes evidence that the body is involved during off-line motor cognitive states such as motor imagery, and consequently simulation possesses an embodied dimension (e.g., through physiological activity; O'Shea & Moran, 2017). Embodiment theories view imagery as its own entity, an embodied process of re-enactment of an action that occurs consciously; accordingly,

these models are less in line with MST and the FEM, which view simulation as process identical to the planning stage of execution, instead aligning with the MCM, considering imagery as a covert process that resembles overt movements to some degree but not in entirety.

2.6 Evidence for Existing Theories

There exist many theories that attempt to explain the neural mechanisms involved in the motor system that result in motor imagery functioning to drive motor learning. Several of these theories share similar tenets with one another; MST and the FEM draw many parallels, and both emulation theory and the forward model build on the concept of feedforward mechanisms. Meta-analyses and reviews previously conducted in efforts to synthesize the available evidence towards the neural mechanisms involved in imagined movement have been limited in sample size (Decety & Grezes, 2001; Munzert & Zentgraf, 2009; Hetu et. al., 2013). In 2018, Hardwick and colleagues conducted a large-scale meta-analysis examining motor imagery, action observation, and overt movement with the aim of providing a quantitative synthesis of the existing literature and comparing the brain networks involved in each modality.

Like many analyses had shown before, the authors found that these modalities share several neural activations. They identified motor imagery as operating predominantly via a premotor-parietal network, with subcortical recruitment of the putamen and cerebellum. Imagery and observation were found to share high overlap of cortical activations in the premotor and parietal regions. Both imagined and overt movement recruited a more diverse range of brain regions compared to observation, including the midcingulate cortex, however during imagery activation of the

midcingulate cortex occurred anteriorly in regions associated with cognitive motor control (Hoffstaedter et. al., 2013), while during overt movement posterior regions associated with more basic motor functions (Picard and Strick, 1996; Procyk et al., 2014) were recruited.

Imagery and overt execution both recruited the putamen, a part of the basal ganglia that is involved in facilitating movement (Ashby & Crossley, 2012; Turner et al., 2003; Shadmehr & Krakauer, 2008), as well as the cerebellum (Hardwick et. al., 2018). Hardwick and colleagues' (2018) analysis revealed consistent somatotopic recruitment of the cerebellum during overt execution, however the same was not observed during imagery, suggesting it's possible that though both modalities recruited the same region, it could be responsible for different functions in each. On a cortical level overt movements recruited sensorimotor and premotor networks, with subcortical recruitment of the thalamus that was not observed during either imagery or observation. These reported cortical activations are consistent with previous literature (Penfield & Rasmussen, 1950; Schlerf et al., 2010; Hardwick et. al., 2013).

Novel to this analysis was the inclusion of a robust discussion of the differences present between imagined and overt movements, including how these differences support or oppose existing theories. Hardwick et. al. (2018) found that during imagery, there is consistent recruitment of the dorsolateral prefrontal cortex (DLPFC), an area involved in executive-level functions related to action preparation (Mars & Grol, 2007; Hardwick et. al., 2018). In contrast the DLPFC was not consistently recruited during overt execution. MST and the FEM suggest that the DLPFC may possibly play a role in inhibiting the execution of overt movements during motor imagery (Blasi et. al., 2006), and may also

be involved in managing working memory demands during imagined tasks (Rogasch et. al., 2015). The MCM argues that the DLPFC is more active during imagined movements due to the increased need for executive-level control of imagined "execution" of the action (Glover & Baran, 2017; Glover et. al., 2020).

While their analysis revealed a consistent sub-network of activation between all three modalities, the activations observed during imagery and observation differed from those seen during overt movement and did not fully align with any of the MST, FEM or MCM theories (Hardwick et. al., 2018). Additionally, the greatest overlap of cortical recruitment was shared between imagined and observed actions, and not imagined and overt movement (although it is worth noting that imagined and overt movement share more cortical activations than observation and overt movement; Hardwick et. al., 2018). As more researchers begin to focus on the theoretical frameworks for motor imagery (e.g., Guillot & Collet, 2005; Munzert & Zentgraf, 2009; O'Shea & Moran, 2017; Glover & Baran, 2017) it is becoming increasingly apparent that the current models are insufficient in explaining the neural mechanisms involved in imagery, and there is a need for research to be directed towards refining current models or the development of new models and theories.

2.7 Fidelity

One area of emerging interest in motor imagery research is that of fidelity. Broadly, fidelity refers to the degree of exactness with which something may be copied or reproduced (Oxford Dictionary). In the context of imagery, fidelity refers to one's ability to accurately reproduce a mental image of a given action. A component of MST, the FEM and the MCM explains that overt actions involve a planning stage, and this

planning is based on stored motor representations (Jeannerod, 1997; 2001; Slifkin et. al., 2008; Glover & Baran, 2017). The mechanics and motor components involved in executing actions that are frequently performed are more familiar than those involved in infrequently performed actions, resulting in refined motor representations that can be imagined more accurately. Thus, according to MST, the FEM and the MCM, imagining a well-known action should result in a higher fidelity image than imagining a task that is mechanistically less familiar or entirely unknown (Jeannerod, 1997; 2001; Slifkin et. al., 2008; Glover & Baran, 2017).

Implications of fidelity are highlighted in studies that implement training prior to experimental task performance. Training offers individuals the opportunity to become more familiar with the mechanisms of movement involved in the completion of an action, building a more accurate representation of that action within their long-term memory stores (Jeannerod, 2001, 2006; Slifkin et. al., 2008). Subsequently, if the individual must call on stored motor representations of that action for imagery performance, they will be able to conjure up a higher fidelity image. Previous research has established that imagined performance of a well-known action results in a more focal pattern of cortical activation compared to performance of unfamiliar actions, which show widespread, bilateral patterns of cortical activation (Doyon et. al., 2003; Floyer-Lea & Matthews, 2005; Kraeutner et. al., 2018). Thus, allowing participants to practice a task prior to the experimental session may affect neural excitability during the experimental task, whereby more practice leads to increased excitability.

Though the idea of motor imagery consisting of only stored, covert actions while physical performance consists largely of overt actions that are monitored and adjusted

with real-time visual and sensory feedback is well established in the literature (Paulignan et. al., 1991; Glover 2004; Glover & Baran, 2017), how covert versus overt actions may be influenced by fidelity has not been directly explored. How image fidelity might impact motor imagery practice can be extrapolated from previous research. For example, a study by Slifkin and colleagues (2008) explored the impact of effector load on movement duration during physical compared to imagined movement, with results showing that as effector load increased, actual movement duration increased. However, while imagined movement duration showed a similar pattern at low effector loads, imagined movements were much longer than actual movements at high effector loads (Slifkin et. al., 2008).

In interpreting their findings, Slifkin et. al. (2008) proposed that low load movements are performed frequently and thus their mechanics are familiar, therefore imagined performance of these movements requires relatively little effort because the movement produces a high-fidelity image, and movement duration mirrors that of actual movements. Comparatively, high load movements are performed infrequently, and their mechanics are unfamiliar, therefore imagined performance of these movements requires increased effort and produces a low-fidelity image, and movement duration is significantly slower than that of actual movements (Slifkin et. al., 2008).

This interpretation is consistent with the MCM, suggesting that during imagined "execution", conscious executive control is involved in monitoring the image as it unfolds, and when image fidelity is lowered due to inability to accurately imagine the mechanics of the movement, functional differences in neural processing occur (Glover & Baran, 2017; Glover et. al., 2020). What Slifkin et. al. (2008) argued in lieu of their results is that the inability to create high-fidelity images becomes problematic at high

levels of force, and this is the reason for the difference in movement duration in their experiment.

Although this study presented very interesting results, there were some limitations to the interpretations. The researchers only used a limited range of loads (0, 5, 10, 20, 40 & 80% maximum voluntary load), so the study provided minimal information on what is happening at higher loads (i.e., in-between 40 & 80% maximum voluntary load). Additionally, the main measure in the study was self-reported movement duration. The use of this self-report measure is problematic for two reasons. First, self-reported movement duration is subject to bias by the participant (Rosenman et. al., 2011); second, while movement duration is the behavioural manifestation of the underlying brain activity, a difference in movement duration between imagined and overt actions only indicates that there is a potential for a difference to exist in brain activity between the two modalities, as it does not measure said activity directly. Obtaining a measure of brain activity would give more insight into the differences between imagined and overt movements during the task and provide further evidence for the mechanisms underlying motor imagery.

While this study did not include a training session within the experimental design, comparing results of similar studies that included training offers further insight into the potential impacts of fidelity on brain activity during imagined movements. One such study used TMS to obtain MEPs during imagined elbow flexion at 10, 30 & 60% of participants' maximum voluntary contraction (MVC; Mizuguchi et. al. 2013). Before the experimental task began, participants took part in a 30-60 min practice session, during which they became familiar with performing the movement at each force level. The

researchers then determined corticospinal excitability during each condition, with results of the study indicating that corticospinal excitability scaled linearly with force; the highest amplitude MEPs were obtained during the 60% MVC condition and were significantly higher than those obtained during the 10% MVC condition (the average amplitude of MEPs obtained in the 30% condition was in-between the average values noted for the 10 and 60% conditions, however it was not significantly different from either).

While this work provided novel insight into the excitability of the nervous system during motor imagery performed at varying forces, there were limitations that should be considered when interpreting the findings, namely that the researchers did not compare the results in the imagery conditions to a group performing the movement overtly. Additionally, only a limited range of forces were used (10, 30 & 60% MVC), meaning the results are not a full representation of scaling of corticospinal excitability across forces (Mizuguchi et. al. 2013).

A similar study examined differences in corticospinal excitability during imagined finger movements in high force compared to minimal force conditions (Helm et. al., 2015). Participants initially underwent a training session to familiarize themselves with the differential forces used throughout the task. Results from this study showed a significant difference between imagery high force and imagery minimal force conditions, and a significant difference between imagery high force and imagery control conditions, with the imagery high force group demonstrating higher average MEP amplitudes than both other conditions. The findings of the research indicate that corticospinal excitability has some sort of positive relationship with force in imagery tasks, such that when force is

increased, the excitability of the cortex is increased as well. Notably, this study did not use an overt movement group to compare results to; rather, they only used an imagery control in which participants imagined a fixation cross on a blank screen. As in both previously discussed studies, there were only a limited amount of force conditions used; high and low, and this does not provide an accurate representation of how corticospinal excitability is scaling as force increases.

Interestingly, the two studies discussed above that found corticospinal excitability during imagined movement scales with force in a similar pattern as in overt movement (Mizuguchi et. al., 2013; Helm et. al., 2015) had participants undergo training of the task at each of the different force levels prior to completion of the experimental task. As discussed, each MST, the FEM and the MCM postulate that overt execution of actions involves a planning stage based on stored motor representations (Jeannerod, 1997; Slifkin et. al., 2008; Glover & Baran, 2017). According to the FEM and MST, imagined performance of an action should match physical performance of an action on a neural level. The findings of Slifkin et. al.'s (2008) research, however, were consistent with these models only during low force movements, when image fidelity is arguably higher than during high force movements (Glover & Baran, 2017; Glover et. al., 2020; Van der Lubbe et. al., 2021).

Recent research that explored the idea of image fidelity as an independent component of motor imagery using fMRI to map brain activity during kinesthetic and visual imagery found that fidelity was uncorrelated to image vividness, i.e., an individual could be kinematically inaccurate at a given task yet still experience vivid imagery (Mizuguchi et. al., 2018). One drawback of this study, however, was that it was assumed

that accurate motor performance indicated accurate motor planning, and therefore accurate imagery. While previous work has measured fidelity as a construct (either directly or indirectly), no research to date has involved the manipulation of fidelity to determine what effects image fidelity may have on the facilitative benefits of motor imagery.

2.8 Force & Effort

Of motor imagery research that has contradicted MST and the FEM, one area that seems to have the most debate surrounding it is that of "effort". As previously mentioned, many studies have been unanimous in concluding that during physical performance of a task, brain activity increases linearly with force (Dai et al., 2001; van Duinen et al., 2008; Perez & Cohen, 2009). Additionally, it has been demonstrated that the amplitude of MEPs obtained following stimulation of finger flexor muscles during an isometric force production task increase as force increases (Muellbacher et. al., 2000; Perez & Cohen, 2009). According to models based on the concept of functional equivalence, brain activity should scale with force in a similar way when this type of task performed via imagery. However, while some research has confirmed that the postulates of MST and the FEM hold true in imagery tasks that manipulate effort (Papaxanthis et. al., 2002; Gentili et. al., 2004; Mizugushi et. al., 2013; Helm et. al., 2015), results of similar studies in the field suggest that functional differences are occurring when effort is manipulated during imagined compared overt movements (Decety et. al., 1989; Park & Li, 2011; Cerritelli et. al., 2000; Slifkin et. al., 2008).

While research on motor imagery and effort has had differing results, it is important to note that many of these studies have varied greatly in their methods,

measures, and definitions of what exactly "effort" is. Given the inconsistencies that exist in the literature, it is important to consider the limitations of previously conducted research in this domain, and how these limitations may have influenced the results. One critical limitation in most previous research is the lack of clearly defined constructs. It should be noted that force and load are each distinct concepts in terms of movement, and each manipulates effector load differently. Altering force manipulates the effector output (Oxford Dictionary), while altering load manipulates the weight experienced (Oxford Dictionary). Effort, on the other hand, is a cognitive construct; the conscious perception of how difficult an individual perceives a task to be (Borg, 1998; Marcora et. al., 2009). Increasing either force or load should (theoretically) increase the perceived effort of a task, however manipulating force involves adjusting effector output relative to an individual's maximum, while manipulating load is not scaled to individual capabilities and is subject to variation between participants. To objectively explore whether corticospinal excitability scales as difficulty of a task increases, it is more beneficial to manipulate force, because percentage of maximum effector output can be held constant across individuals, whereas varying loads may be more/less difficult between individuals based on their ability.

Further adding confusion, the methods employed to test these concepts in the literature are varied. For example, the studies by Mizuguchi et. al. (2013) and Helm et. al. (2015) discussed previously did not compare imagined movements to physically executed ones and included a training block prior to the experimental session. Additionally, the work by Helm and colleagues (2015) ambiguously tested participants at high and low force levels. Many studies in this domain have focused on behavioural measures such as

mental chronometry (e.g., Decety et. al., 1989; Cerritelli et. al., 2000; Papaxanthis et. al., 2002; Slifkin et. al., 2008) which, though providing a valuable foundation for further research, cannot directly evaluate what is occurring on a neural level. Additionally, many of these studies mention effort but do not objectively define what effort is, and the use of force vs. load makes it difficult to compare between research (i.e., how comparable is measuring duration of imagined movements with a weighted backpack to duration of imagined finger flexion at varying percentages of MVC?).

These limitations highlight the varying methodology and measures used in studies that have explored the relationship between brain activity and "effort" during motor imagery. Given these differences it is unsurprising that some results are contradictory to one another. Most notably, there seem to be many studies that use differing methods to manipulate task difficulty; for example, Helm et. al. (2015) considered high force to be movement with a fixed resistance, achieved via finger movement against a spring, while Mizuguchi et. al. (2013) used a torque meter to determine participant's MVC, and used that maximum to obtain 10, 30 and 60% force levels relative to each participant. Slifkin et. al. (2008) used custom-designed finger weights to manipulate load during finger movements, while Decety et. al. (1989) used backpacks with a pre-determined weight of 25kg to manipulate load. Given the limitations in previous literature, the current study utilizes force, where force is defined as the effector output exerted on a transducer. Force will be manipulated as a percentage of an individual's maximum output (i.e., where gripping at 50% force is gripping at 50% of each participant's MVC).

Chapter 3: Objectives & Hypotheses

3.1 Objectives

The above sections have presented an argument that current evidence does not fully support any of the proposed models for motor imagery, and though advances in functional imaging and connectivity investigation techniques offer the opportunity to explore the mechanisms of imagery more closely on a neural level, the exact neural mechanisms involved in this modality are not known. The concept of image fidelity offers a new avenue for exploration of motor imagery. Exploring how image fidelity affects corticospinal excitability during task performance can provide insight into the neural mechanisms involved in task simulation and whether they differ between imagined and overt movements. Furthermore, understanding the role of image fidelity in imagery practice could be crucial in prescribing motor imagery as a therapeutic treatment.

It is the goal of this research to provide an explanation for the divide in the current literature on how brain activity scales at varying forces in imagined compared to overt movements, and to offer supporting evidence to the theoretical underpinnings of why motor imagery is effective for motor skill acquisition. To accomplish these objectives, this study measured corticospinal excitability during both imagined and overt performance of a grip task in which participants gripped a transducer at varying percentages of their MVC. Participants were not exposed to the task prior to the experimental session, during which they were randomly assigned to one of two groups; one that completed the task overtly and then via imagery, and one that completed the task via imagery and then overtly. These assignments delineate high-fidelity and low-fidelity conditions respectively. Participants completed the task at a range of forces, gripping the transducer at 10% through 80% of their MVC in 10% increments (for a total

of 8 levels of force), to obtain accurately scaled results. TMS was used to elicit MEPs as a measure of corticospinal excitability throughout the task (Stinear & Byblow, 2003), with one MEP recorded during grip in each trial.

Manipulating the order in which participants completed the task (i.e., via imagined or overt execution first, then the opposite modality) allows for comparison of i) differences in scaling of corticospinal excitability between imagined and overt task performance and ii) differences in scaling of corticospinal excitability between participants who first performed the task physically (high-fidelity imagery group), and those who first performed the task via imagery (low-fidelity imagery group). Investigating whether image fidelity affects the scaling of brain activity across forces in imagined compared to overtly executed movements offers insight on how the current theories of motor imagery fit with the actual mechanisms of imagined movement. Collectively these results will inform on the use of imagery for motor skill acquisition.

3.2 Hypotheses

To answer the research objectives this study explored three main hypotheses. Firstly, in determining corticospinal excitability during covert movement, hypothesis one predicted that MEP amplitude would demonstrate a positive and linear trend with force, whereby higher forces will produce larger MEPs. Secondly, hypothesis two predicted that during motor imagery the trend between MEP amplitude and force would be linear at low forces but plateau at higher forces. Lastly, hypothesis three predicted that MEP amplitude would be more similar between imagined and overt performance in the high-fidelity (i.e., when participants perform the movement physically before performing it mentally) compared to the low-fidelity group.

Chapter 4: Methodology

4.1 Participants

This study involved the first use of a comparison of corticospinal excitability at different effector outputs performed via imagery and overt movement. As such, no previous literature existed upon which to estimate expected effect sizes for a power analysis; instead, a power analysis was performed assuming a moderate effect size ($f = 0.40$) to determine the required sample size at $ß = 0.8$, $\alpha = 0.05$. For a mixed-model ANOVA, we required a sample size of 54 (27 per group) which is in line with previous studies assessing brain excitability during motor imagery (Stinear et. al., 2006; Williams et. al., 2012). Consequently, this study sought to recruit a total of 60 participants to account for potential issues with data collection including the inability to locate a motor hotspot (via TMS), an occurrence noted in a small percentage of participants.

All participants were over the age of 17 with normal/corrected-to-normal vision, in good health (no neurological injury/disease as reported by participants) and TMS eligible (as determined by the standard TMS screening form; Rossi et. al., 2021). Participants were pseudorandomized into one of two groups, differing only in order of experimental conditions (high-fidelity: overt-imagined performance; low-fidelity: imagined-overt performance). Demographic information, such as age, sex and handedness was collected to characterize the sample. The study had approval from the Dalhousie University Health Science Research Ethics Board (REB# 2019-4871).

4.2 Questionnaires

4.2.1 Kinesthetic Visual Imagery Questionnaire (KVIQ)

The KVIQ is a questionnaire used to assess the intensity and clarity with which an individual can perform motor imagery based on a self-rating scale (Malouin et. al., 2007; Appendix A). The KVIQ assesses imagery clarity using self-ratings of visual imagery, while imagery intensity is assessed by self-ratings of kinesthetic imagery (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 assessment, 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, they were required to physically perform the movement as had been demonstrated to them. Second, they were asked to imagine the movement via visual (third person) imagery, whereby the participant imagined what it looks 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, they were asked to imagine the movement via kinesthetic (first person) imagery, whereby the participant imagined what it feels like when they themselves perform the movement. Following kinesthetic imagery of the movement, the participant was 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 participants ability to perform imagery, not as a screening tool.

4.2.2 TMS Screening Form

All participants were screened for contraindications to TMS using a standard screening form (Rossi et. al., 2021; Appendix B). Participants were excluded from the study if they answered yes to any of the first 7 questions, if they had a history of i) problems with TMS or magnetic resonance imaging (MRI) or ii) fainting spells, or if they had metal implanted in their brain/skull.

4.3 TMS Procedures

Single-pulse TMS was administered to the cortical representation of the flexor digitorum superficialis (FDS) 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 BiStim^2 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 pre-auricular (LPA), right pre-auricular (RPA), glabella and tip of the noise 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 centre

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. For participant safety as outlined in the study REB document, a maximum stimulator output intensity of 50% was not surpassed during the experimental session. This value was chosen by the lead experimenter based on their familiarity with the equipment and previous experience running similar studies, where stimulation at an output greater than 50% on the Magstim BiStim^2 system often results in activation of musculature in the head/face regions that can 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.

RMT is defined as the minimal stimulation intensity at which the target muscle produces an MEP with amplitude ≥ 50 μV in a minimum of five out of ten trials. Beginning at point 3,3 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 3,3 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 both location and stimulation intensity were determined the experimental task began. During the task, single pulse TMS was applied at 120% RMT 5sec into each trial. 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 using Signal software and associated hardware (Signal 6.03c, and Power 1401; Cambridge Electronic Design, UK).

4.4 Electromyography (EMG)

Motor evoked potentials were obtained from the FDS muscle during TMS. The FDS, a long flexor of the digits, was located by moving approximately 5cm distal to the elbow crease on the anterior aspect of the forearm and palpating while the participant repeatedly performed a gripping motion (i.e., finger flexion). Once located, two surface EMG electrodes were placed on the skin overlying the FDS muscle with a 1cm interelectrode distance. Electromyography was collected throughout both blocks of the experimental task using Signal software (Signal 6.03c, 1902 amplifier and Power 1401; Cambridge Electronic Design, UK) sampled at 1000 Hz with a bandpass of 10-500 Hz.

4.5 Force Transducer

The transducer and power supply used to measure grip force was a DC 750 series linear variable differential transducer (DC-LDVT; Schaevitz Sensors©). The sensor had a diameter of 19mm and was calibrated using a linear calibration curve (Figure 2B). The transducer was mounted in a custom-made device that stood upright and contained a handle for participants to easily grip and squeeze at the target force levels (Figure 2A). Output from the force transducer was sampled at 1000 Hz using custom programmed LabVIEW software and associated hardware (USB 6251 DAQ, BNC-2090A and LabVIEW 2019 SP1, National Instruments Corp., TX) for visualization purposes and via Signal software for offline analysis of force data.

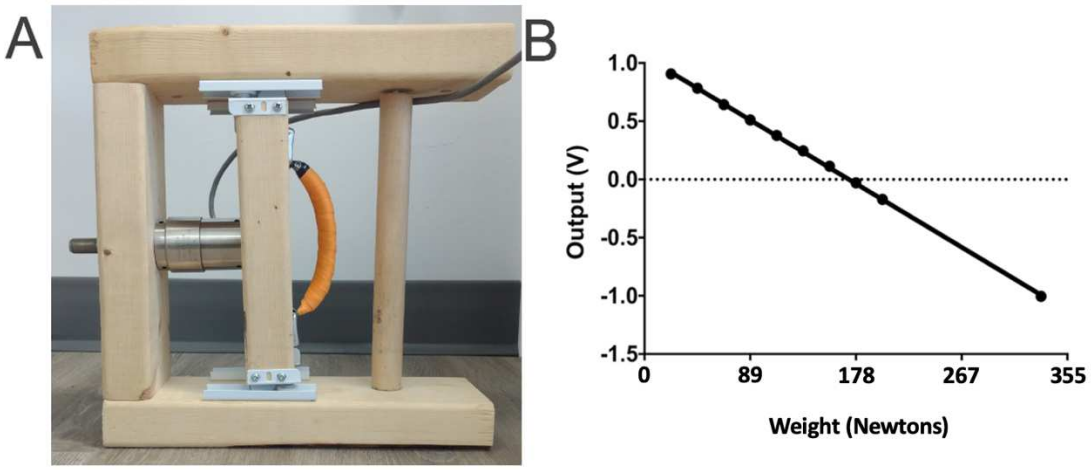

Figure 2. Transducer Apparatus & Calibration Graph. (A) The custom-built apparatus containing the force transducer. Participants placed their palm on the wooden dowel and wrapped their fingers around the orange handle. Squeezing their hand around the handle and dowel simulated grip and generated force. (B) The linear calibration curve used to translate voltage outputs from the transducer into a unit of force (Newtons).

4.6 Experimental Session

The study consisted of a single 2-hour long session. The first 15 minutes were devoted to an overview of the study, informed consent, TMS screening and completion of the KVIQ. The next 30-45 minutes were used to set the participant up for TMS and to determine their motor "hotspot". The experimental session lasted approximately 50 minutes, consisting of two blocks: one imagined performance block and one overt performance block. Each block contained 80 trials, with rest periods distributed within blocks such that participants had 2min of rest every 20 trials. Between blocks there was a 4min rest period, during which the participant was given instructions for the second block

(Figure 3). Following the session all participants were debriefed and compensated for their time.

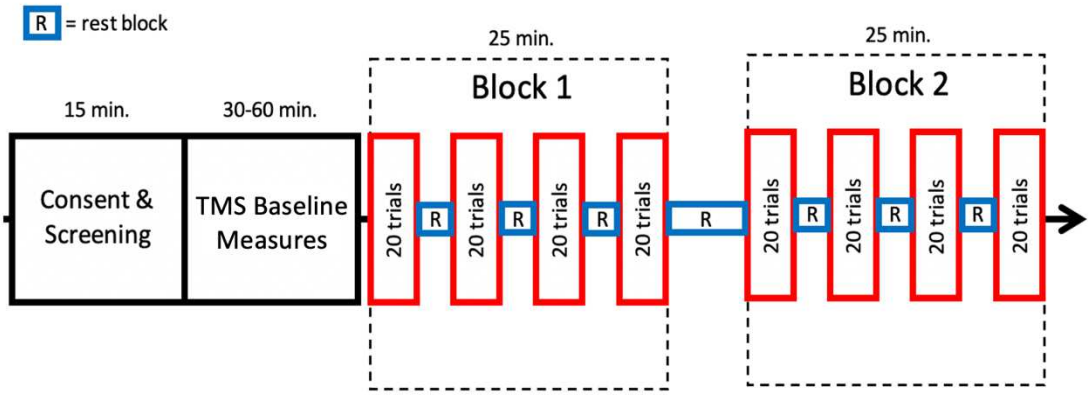

Figure 3. Experimental Block Structure. The structure and timeline of the experimental session is depicted. The first two squares show the time estimated for consent & screening, and TMS baseline measures. The second two squares show the two blocks of the experimental task. Each block consisted of four sets of 20 trials, with each set of trials separated by 2min of rest. A 4min rest period was provided in-between blocks to give instructions to the participant before the second block began.

4.7 Experimental Procedures

4.7.1 Experimental Task

Each participant completed 160 trials of the grip task; the session was split into two blocks, such that 80 of the trials were physically executed by the participant and 80 were imagined. The task was performed using a handheld force transducer, whereby the mechanical force produced by the participant gripping the apparatus was translated into a voltage, which was read into custom-programmed software and presented to the participant (described below). Prior to the experimental task, participants performed a maximal force test to determine their MVC, during which they were instructed to grip the

force transducer with maximal effort for 3sec. The transducer was oriented such that participants had their upper arm straight down their side, with their elbow positioned at 90 degrees of flexion and their forearm resting on the arm of the chair. Participants were instructed to grip only with their hand, avoiding twisting their arm or lifting the transducer. Pilot testing revealed that participants generally demonstrated poor form during the maximal force test, often leaning into the transducer or tilting the apparatus to the side to achieve a more forceful grip. Consequently, to correct for potential biasing of force output on the first grip, the maximal force test was designed such that each participant performed this test three times, and the average of these three trials was used to determine their MVC value. If participants demonstrated poor form on the first test, the experimenter corrected them prior to the second two tests to ensure that the maximum value accurately represented their abilities.

During the experimental session participants were tested at 10, 20, 30, 40, 50, 60, 70 & 80% of their MVC. Participants were pseudorandomized into one of two groups; a high-fidelity group that completed the task in the block order of overt-imagined performance, and a low-fidelity group that completed the task in the block order of imagined-overt performance (Figure 4). Each block consisted of 10 trials at each grip force (totalling 80 trials). The grip force order was pseudorandomized through the first block, and this randomized order was repeated in the subsequent block. This pseudorandomized order was designed to avoid several back-to-back trials at high force levels to reduce the risk of fatigue in both the overt and imagery blocks, since central fatigue has been shown to have a decremental effect on MEP amplitude (Brasil-Neto et. al., 1993; 1994).

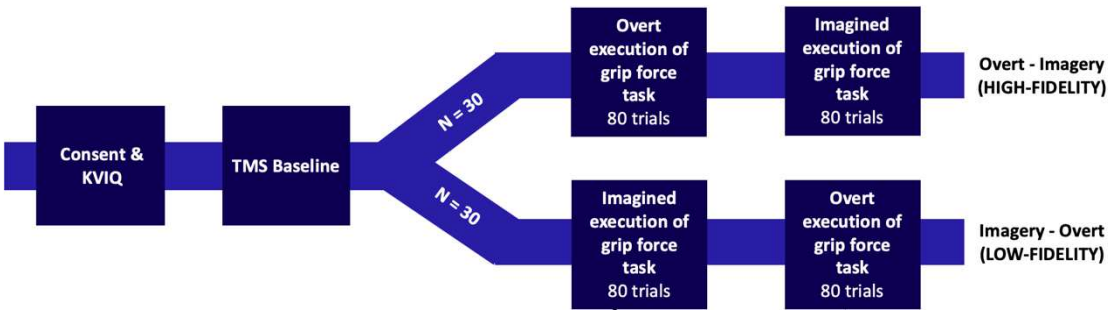

Figure 4. Experimental Session Structure. An illustration of the experimental session is displayed. Divergence in the line represents where the participants are divided into the high-fidelity (seen topmost in the image) and low-fidelity (seen bottommost in the image) groups. Aside from the block order, there was no difference in the session structure between groups.

4.7.2 Block Structure

Prior to the first block participants were read an instruction script detailing the objectives of the block (outlined below; for full scripts see Appendix C). During the task, participants were seated comfortably in a chair, with their non-dominant hand rested on their lap, and their dominant hand gripping the transducer. During the session the transducer was situated based on each individual participants position in the TMS chair and strapped to a table that was adjusted in height to align with the participant's hand. Each trial consisted of a single grip of the force transducer either via imagined or overt execution.

In total, each trial lasted 11sec (see the timeline of an individual trial in Figure 5B). A monitor placed in front of the participant signaled the beginning of each trial by a light-cued 3sec countdown, where lights displayed on the monitor flashed red, then yellow, then green (each light was "on" for 1sec; see Figure 5A). The participants were

instructed to begin gripping when the light turned green, and the monitor displayed the word “Go!”. The target force appeared on the monitor at the start of each trial when the red light flashed on, so the participant had 3sec to read which target force they were required grip at for the next trial. Upon the “Go!” cue participants had 2sec to grip the force transducer with the appropriate force (Figure 5B).

In the overt execution block, force output was guided by a simple meter on the monitor. The meter was marked vertically with numbers 0-100 and filled with a blue bar depending on the force the participant applied to the transducer (i.e., if one was gripping at 50% of their MVC the meter would fill halfway, to the 50 mark; Figure 5A). Participants were instructed to maintain the force that resulted in the meter filling to the target percentage throughout the trial (Figure 5A). Following the 2sec allotted for aligning force to the target, a single pulse was delivered via TMS to elicit an MEP (described in section 4.3 TMS Procedures; Figure 5B).

During the imagined execution trials participants had the same light cues and meter displayed on the monitor in front of them and were given the same instructions as during the overt execution block (to imagine themselves gripping the transducer at the required force and maintaining that force until stimulation occurred) however they had no visual feedback from the meter as they were not physically gripping the transducer. All participants were instructed to place their hand on the transducer while performing imagery, oriented in the same position as during the physically performed trials. Participants were asked to perform imagery with their eyes open, to match the overt condition as closely as possible, and to ensure that they would see the target force and the

countdown that was displayed on the monitor. Following stimulation, there were 6sec of rest on the back end of the trial before the next trial began (see Figure 5B).

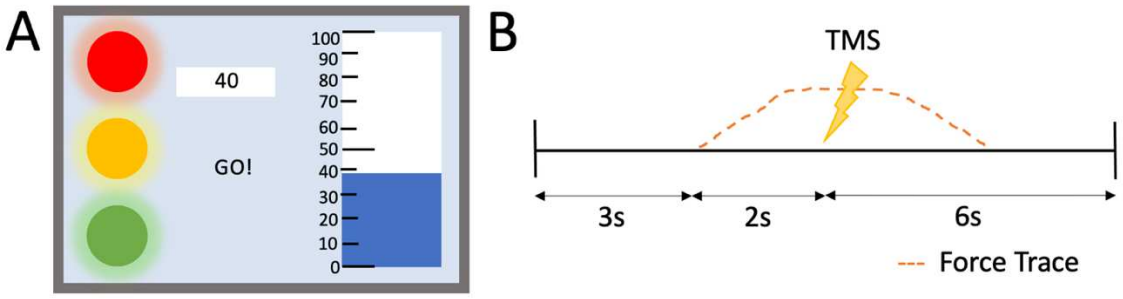

Figure 5. Monitor Display for Experimental Task. (A) An illustration of the monitor displayed to participants during the experimental task is shown. The lights on the left flashed a countdown of red, yellow, green (3, 2, 1), after which the word "Go!" appeared above the target force, which is 40% MVC in this example. The bar on the right filled with blue as the participant adjusted their grip, where a full bar indicated gripping at 100% MVC. (B) Timeline of an individual trial. Each trial was 11sec long. Following 3sec to read the target force and prepare, participants had 2sec to obtain the desired grip force. 5sec into the trial a single pulse of TMS was administered to elicit an MEP. Following stimulation there were 6sec on the back end of the trial before the next trial began.

4.8 Data Analysis

4.8.1 MEP Analysis

The primary outcome measure of this study was the comparison of MEP amplitude (i.e., corticospinal excitability) between forces. EMG data obtained during the session was exported to a CFS file from Signal, bandpass filtered at 10-500 Hz and rectified to isolate the envelope of muscle activity (Kraeutner et. al., 2016). Background EMG was obtained by calculating the mean EMG activity during a 1sec window prior to the onset of stimulation during imagery trials. We define EMG threshold as background EMG activity during a rest period ±2 standard deviations; any EMG activity surpassing

this threshold in the imagery block was excluded from analysis. In addition, if more than 33% of trials were removed from analysis due to excessive background EMG activity, the participant was excluded from further analysis. All EMG analysis was performed using custom software programmed in R.

To calculate the peak-to-peak amplitude of MEPs, raw EMG signals were uploaded to custom R scripts that have been used previously in our laboratory for analyzing Signal data. In general terms, the custom scripts isolated the time window in which the MEP should have occurred and placed a set of cursors 10ms and 50ms post the TMS pulse, with the software returning the peak-to-peak amplitude (i.e. the difference between the maximum and minimum values) in that specified time period. This timing accounts for conduction time and the duration of the MEP. Data was visually inspected to ensure that the cursors captured the negative and positive peaks related to the MEP, and not artifact related to the TMS pulse.

Trials in which the script-determined minimum value of the MEP occurred before the maximum value were labelled as atypical (since the expected pattern for the standardized MEPs is peak-valley). For the overt execution trials the raw EMG data was filtered at 10-500 Hz and the MEP was isolated; any trials in which the MEP could not be detected or was identified as atypical were discarded. For the imagery trials, the background EMG data was also analyzed for excessive movement (defined above), and any trials in which participants exceeded the predetermined criteria of background EMG activity surpassing ±2 standard deviations from the mean, or in which MEPs were identified as atypical were excluded from further analysis.

Considering the high variability of MEP amplitude when participants are not engaged in any cognitive or motor activities (Kiers et. al., 1993) a measure of MEP amplitude at rest was not obtained. Instead, each individual participants data was standardized using a z-score transformation, such that the mean MEP amplitude obtained across all trials in each condition was zero with a standard deviation of one. This type of transformation is in line with previous MEP analysis techniques used in imagery studies, where researchers have performed similar transformations as a means of standardizing MEP amplitudes across participants (e.g., Aglioti et. al., 2008; Wright et al., 2014; Bruton et. al., 2020).

4.8.2 Force Data Analysis

Transducer data was exported to a CFS file from Signal; exported data included the target force, and the force trace during the trial. The achieved force was determined by taking an average of the voltage values obtained during a 200ms window prior to the onset of stimulation (i.e., the end of the force trace, 1.8s after the participant initiated grip). This window was selected based on visual inspection of the data collected during pilot testing and with regard to the timing of the TMS pulse. Trials in which the achieved force was greater/less than the target force $\pm$2.5% were excluded from further analysis.

4.8.3 Statistical Analysis

A mixed-model ANOVA was used to determine both within and between groups differences in the data. To address the primary research question, MEP amplitude (i.e., corticospinal excitability) was compared during imagined and overt conditions at each force level, reporting main and interaction effects. Post-hoc analyses were used to determine at which forces (if any) corticospinal excitability differed within imagined and

overt conditions respectively. To address the secondary research question, MEP amplitude across factors (where the between-group factors were condition and order, and the within-groups factor was force) was compared. All statistical analyses were performed using a custom R script with an a priori alpha of $p < 0.05$ denoting significance.

Chapter 5: Results

5.1 Participant Demographics

Data collection was ongoing at the time of writing this thesis, with a total of 43 participants recruited to date; in 10 of these participants TMS hotspotting could not establish a reliable RMT measure of the FDS muscle, and consequently these participants could not participate in the experimental task. Of the 33 participants in which FDS hotspotting was successful, one participant was excluded from analysis due to an equipment error during data collection that polluted the force transducer data, and another participant was excluded from analysis due to an inability to accurately achieve the target force in >50% of trials. After data cleaning, 31 participants (20 = female, 27 = right-handed) remained. The age of participants ranged from 18-24 (M = 21, SD = 2.21), and the kinesthetic scores on the KVIQ ranged from 15-25 (M = 21.55, SD = 3.09), indicating that all participants self-reported a moderate-excellent ability to perform kinesthetic motor imagery (Malouin et al., 2007). The group sizes for the high and low-fidelity conditions were n = 16 and n = 15 respectively. All demographic information collected in the study is reported fully in the supplementary data in Table S1.

5.2 Force Data

Each participant's maximum output on the force transducer (measured during the max test at the beginning of the experimental session) was used to calculate the force exerted on the transducer during each trial as a percentage (described in methods). Transducer data from each individual trial was measured during a 200ms window prior to the onset of stimulation. On average, participants were highly accurate at achieving the

target force at all levels (Figure 6), with average accuracy ranging from 96.03% (at 10% force) to 97.24% (at 30% force).

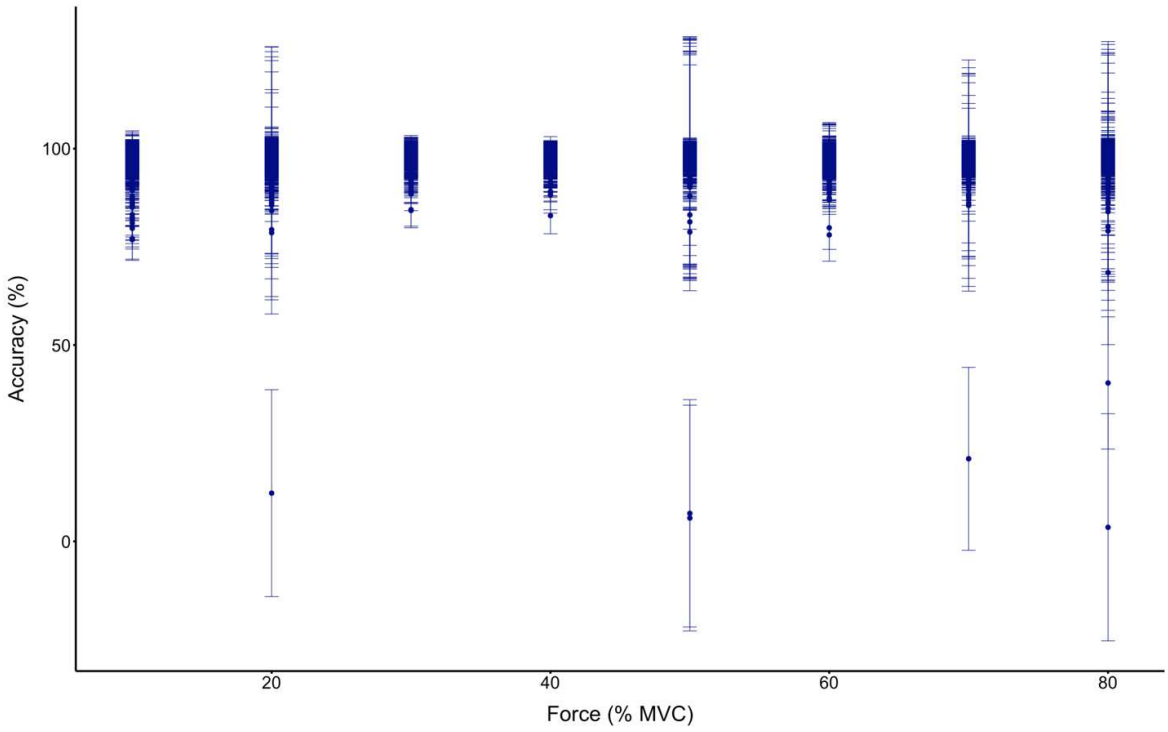

Figure 6. Force Accuracy. A graph plotting accuracy (taken from individual, not pooled data) in each trial is shown for each force level, with error bars showing the standard deviation. The points seen at very low accuracy are trials that were dropped from further analysis.

While it was initially proposed that any trials in which the achieved force did not fall between ±2.5% of the target would be excluded from further analysis, a visual inspection of the data revealed that increasing to ±3% resulted in the preservation of 162 additional trials in comparison to the stricter criteria. Since ±3% of the target force still allowed each level to have discrete windows (i.e., the 10% target ranges from 7-13%, the 20% target ranges from 17-23%... etc.), this criterion was adopted. With 31 participants

completing 10 trials at each force level in the overt execution condition, there were 310 trials at each force to be used for the transducer data analysis. Applying the new criterion (target ±3%) resulted in a total of 254, or 5.12% of trials, being excluded from further analysis. The number of successful trials at each force level ranged from 230 to 310; all participants successfully achieved the target in all trials at the 10% level, while 80 trials were dropped at the 80% level due to failure to achieve the target. There was a negative linear relationship between achieving the target and force level (Figure 7).

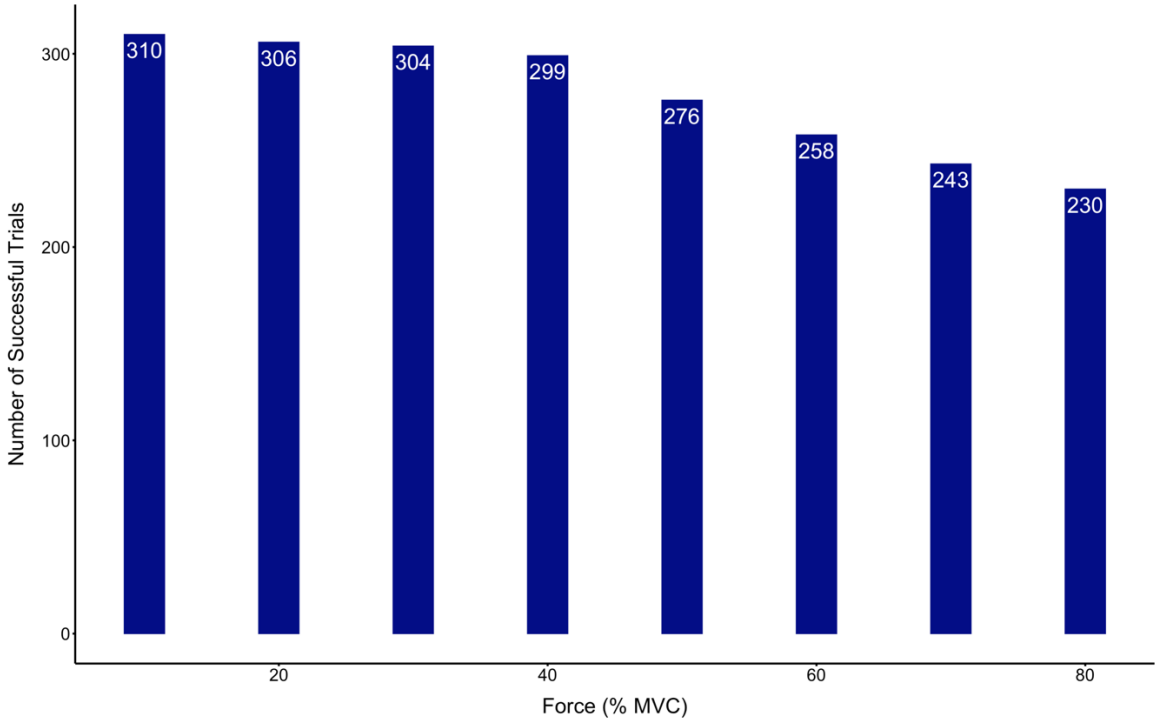

Figure 7. Successful Trials after Transducer Data Analysis. The number of successful trials (i.e., trials in which the target force was achieved) following the filtering of the transducer data is shown for each force level. The raw data contained 310 trials at each force level. Each bar contains the number (seen in white) of trials that remained following the exclusion of trials in which the target force was not achieved.

5.3 EMG/MEP Data

EMG data was filtered and MEPs were calculated as described in the methods. As in the overt execution data, there were 310 trials at each force level in the imagery data to be used for EMG analysis, in addition to the trials that remained in the overt execution data once the transducer data had been filtered for successful trials (Figure 7). After filtering and cleaning, 301 trials were dropped from the imagery data due to meeting the atypical criteria for MEPs and/or exceeding the threshold for acceptable EMG activity while at rest, and a further 62 trials were dropped from the overt execution data because they met the atypical criteria for MEPs. In total, the EMG data analysis resulted in 363 trials (7.32%) being excluded from further analysis.

The number of successful trials at each force level in the imagery data ranged from 267 to 280 and was consistent across force levels. In the overt execution data, the number of successful trials ranged from 221-304, and each increase in force level had a corresponding decrease in number of successful trials (Figure 8; note that this trend was observed after cleaning of the transducer data, and the filtering/cleaning of EMG data did not change this trend).

After all data cleaning and filtering, a total of 4,343, or 87.56% of trials were classified as successful and used for analysis. 6.37% of excluded trials were from the overt execution data and 6.07% from the imagery data. A greater number of trials were preserved in the overt execution data at lower force levels, with more trials dropped at higher forces; in the imagery data trials were excluded evenly across force levels.

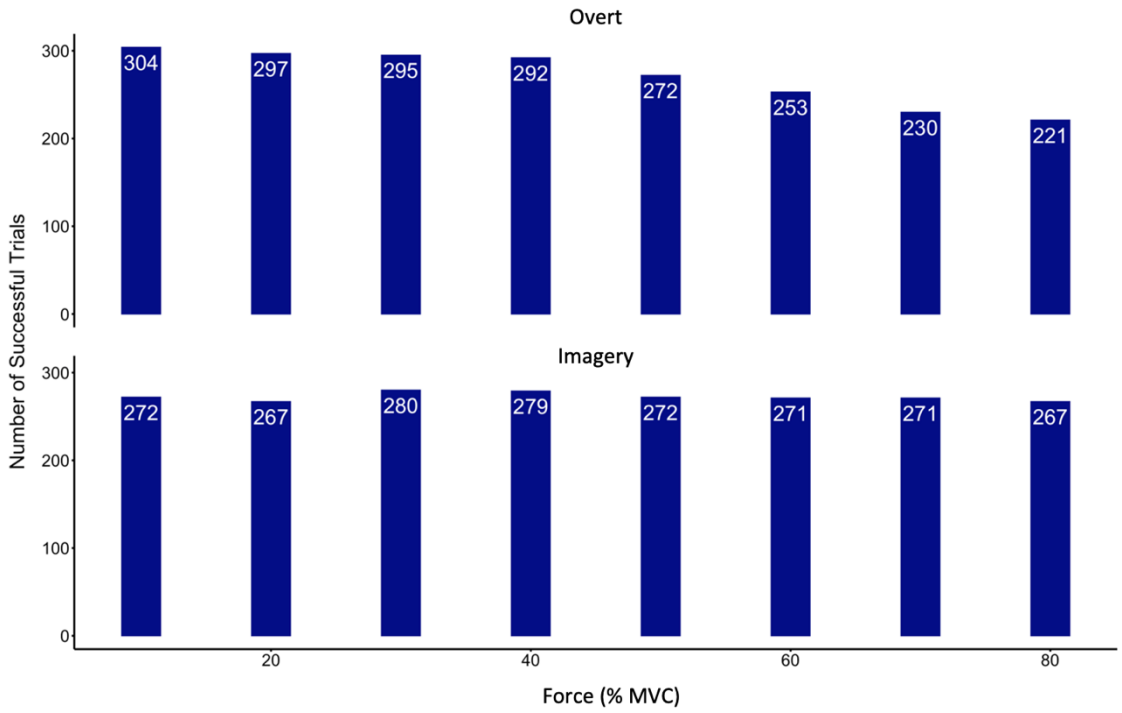

Figure 8. Successful Trials after EMG Data Analysis. The number of successful trials following the filtering of the EMG data is shown for each force level, separated by modality. The raw data contained 310 trials at each force level. The overt execution data was filtered from the successful trials remaining after the transducer data analysis. Each bar contains the number (seen in white) of trials that remained following the exclusion of trials in which the MEP was atypical, or (exclusive to the imagery condition) excessive background EMG activity was detected.

5.4 Z-Score Transformation

A mixed-model ANOVA was used to determine within and between-group differences. As expected from previous research (i.e., Stinear & Byblow, 2003), the magnitude of MEPs observed during overt execution was much larger than those observed during imagery, and there was greater variance observed in the overt execution condition compared to the imagery condition (raw data is shown in Figure S1). Consequently, to compare between groups using an ANOVA, the data for each individual participant was standardized using a z-score transformation for each modality. The mean

(μ) and standard deviation (σ) of MEP amplitude was determined for each individual participant in each condition. The mean MEP amplitude was subtracted from each MEP value (x), and that value divided by the standard deviation to generate a z-score value (Z; see Figure 9). As a result, the mean MEP amplitude for each individual was centered around zero in both the imagery and overt conditions, with a standard deviation of one. The z-score transformed data met the assumptions for normality and homogeneity of variance (Figure 10).

$$Z = \frac{x - \mu}{\sigma}$$

Figure 9. Z-Score Equation. The equation used for z-transforming the data is shown.

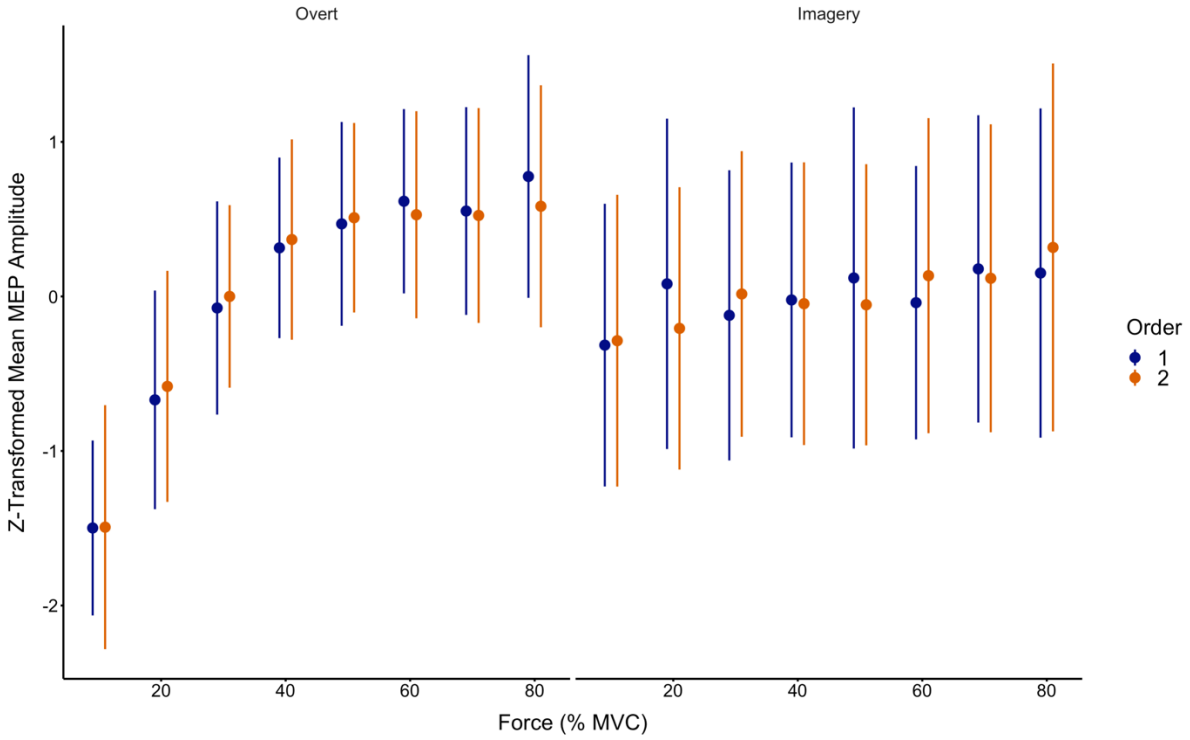

Figure 10. Z-Score Transformed Data. Mean MEP amplitude at each force level in overt (left panel) and imagery (right panel, MI) conditions following the z-score transformation. Error bars show the standard deviation. The blue points represent data that was collected during the first block and the orange points represent data collected during the second block; this data is separated in the graph to highlight the effects of the fidelity manipulation in the imagery group.

5.5 Main Effects and Interactions

The data was analyzed in R using the ezANOVA command, where the mean MEP amplitude of the z-score transformed data was compared between modalities and order, with within-group comparisons of force. The output of the test is reported fully in the supplementary data (Figure S3).

5.5.1 Hypothesis 1: MEP Amplitude during Overt Execution

There was a significant main effect of modality ($F(1, 56) = 8.545$, $p = 0.005$, partial $\eta^2 = 0.005$), and a significant main effect of force (note that since sphericity is violated Greenhouse-Geisser corrected results are reported ($\varepsilon = 0.544$); $F(3.808, 110.432) = 64.93$, $p < 0.001$, partial $\eta^2 = 0.529$) on MEP amplitude. There was a significant interaction effect between modality and force (Greenhouse-Geisser corrected results are reported ($\varepsilon = 0.544$); $F(3.808, 110.432) = 32.246$, $p < 0.001$, partial $\eta^2 = 0.358$). There were no other significant interactions observed in the data. The interaction between modality and force is shown in Figure 11.

Given the significant interaction between modality and force, post hoc analyses were run to determine differences between levels of force. In the overt execution condition, post-hoc comparisons showed that MEP amplitude at 10% force was significantly different than MEP amplitude at all other force levels; this was found for 20, 30, and 40% forces as well. The mean MEP amplitude observed at 50% force was not significantly different than the mean MEP amplitude at 60 or 70% but was significantly different than that observed at 80% force. There was no significant difference between mean MEP amplitude at 60 and 70% forces, or 60 and 80% forces, however there was a significant difference between mean MEP amplitude at 70% compared to 80%. All post-hoc comparisons between levels of force during overt execution are reported in Table 2.

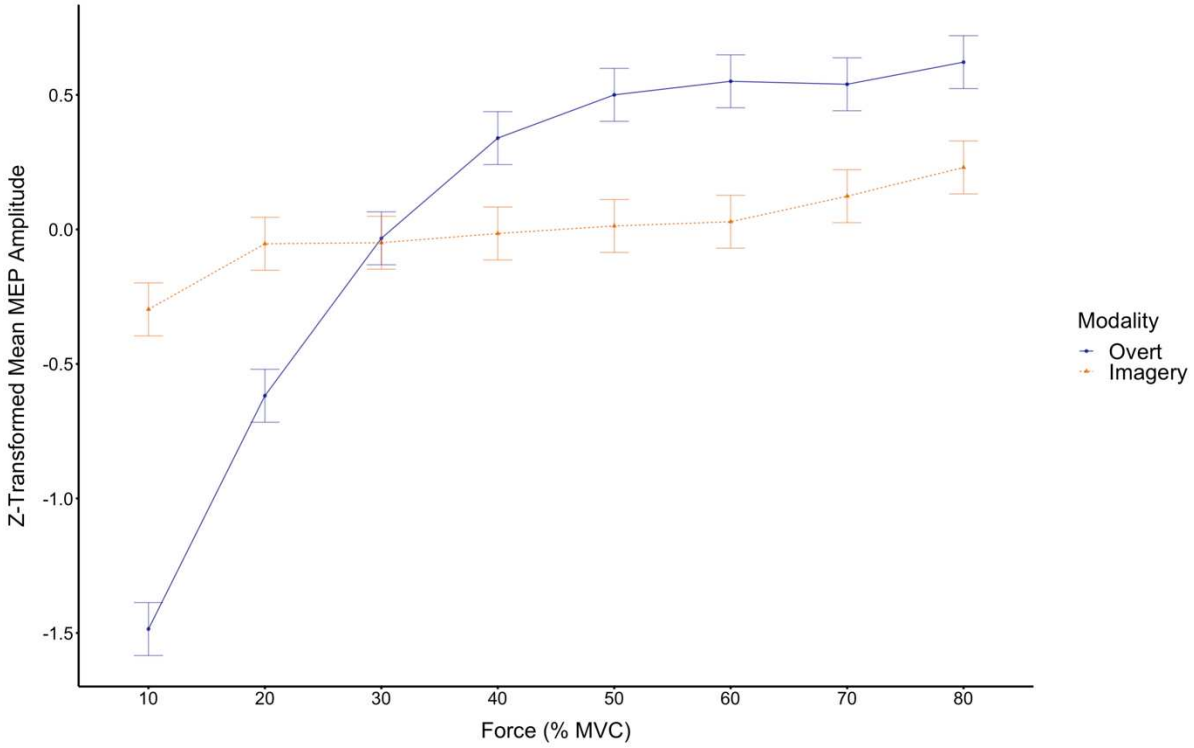

Figure 11. Interaction Effect for Force ~ Modality. A plot visualizing the interaction between force and modality is shown, with the imagery condition seen in orange and the overt execution condition in blue. Error bars around the means show fisher's least significant difference.

Table 1. Post-hoc Comparisons Between Forces – Overt. *t*-tests comparing forces for the overt execution condition are shown. Bonferroni corrected p-values were used to determine significance.

Force Comparison	p	Significance
10vs20	<0.001	***
10vs30	<0.001	***
10vs40	<0.001	***
10vs50	<0.001	***
10vs60	<0.001	***
10vs70	<0.001	***
10vs80	<0.001	***
20vs30	<0.001	***
20vs40	<0.001	***
20vs50	<0.001	***
20vs60	<0.001	***
20vs70	<0.001	***
20vs80	<0.001	***
30vs40	<0.001	***
30vs50	<0.001	***
30vs60	<0.001	***
30vs70	<0.001	***
30vs80	<0.001	***
40vs50	0.0058	**
40vs60	<0.001	***
40vs70	0.0013	**
40vs80	<0.001	***
50vs60	0.1484	
50vs70	0.5045	
50vs80	0.0039	**
60vs70	0.4957	
60vs80	0.0969	
70vs80	0.0298	*

5.5.2 Hypothesis 2: MEP Amplitude during Imagery

As reported above, there were significant main effects of modality and force, as well as a significant interaction between modality and force. *t*-tests performed using Bonferroni corrected p-values found that in the imagery condition, there was a significant difference between the mean MEP amplitudes at 10% force compared to all other levels. There was a significant difference between the mean MEP amplitudes at the 20, 30 and

40% levels compared to the mean MEP amplitudes observed at both 70 and 80% forces, and a significant difference between the mean MEP amplitudes at 50 and 60% forces compared to the mean MEP amplitude at 80%. All post-hoc comparisons between levels of force during imagery are reported in Table 1.

Table 2. Post-hoc Comparisons Between Forces – Imagery. t-tests comparing force levels for the imagery condition are shown. Bonferroni corrected p-values were used to determine significance.

Force Comparison	p	Significance
10vs20	0.0085	**
10vs30	0.0081	**
10vs40	0.0021	**
10vs50	<0.001	***
10vs60	<0.001	***
10vs70	<0.001	***
10vs80	<0.001	***
20vs30	0.8988	
20vs40	0.8022	
20vs50	0.3267	
20vs60	0.2465	
20vs70	0.0148	*
20vs80	0.0014	**
30vs40	0.6881	
30vs50	0.2462	
30vs60	0.1755	
30vs70	0.0071	*
30vs80	<0.001	***
40vs50	0.4283	
40vs60	0.3280	
40vs70	0.0192	*
40vs80	0.0018	**
50vs60	0.8801	
50vs70	0.1442	
50vs80	0.0225	*
60vs70	0.1766	
60vs80	0.0278	*
70vs80	0.3473	

5.5.3 Hypothesis 3: MEP Amplitude & Fidelity

Analysis revealed no main effect of order ($F(1, 56) = 0.003$, $p = 0.952$, partial $\eta^2 < 0.001$) on MEP amplitude during imagery performance. Likewise, there were no significant higher-order interactions in which order was a factor. No post-hoc analyses were performed given the null findings.

Chapter 6: Discussion

This study aimed to determine how corticospinal excitability scales over increasing forces during the overt execution of a motor task compared to imagery, and furthermore sought to explore how image fidelity affects corticospinal excitability during motor imagery performance. The overall objective of this thesis was to further our understanding of the mechanisms involved in motor imagery performance and contribute to the knowledge of how motor imagery can be used to increase corticospinal excitability and promote motor learning.

In designing this study, we sought to address gaps in the literature including the lack of a direct comparison between imagery and overt execution groups, unclear definitions of how "effort" was being manipulated, use of indirect measures of brain activity (such as mental chronometry), and the lack of a full range of forces/loads being tested. Furthermore, we sought to offer an analysis of how the findings of the present study align with the theories proposed to explain motor imagery, including the dominant theories centered on functional equivalence (FEM and MST), the recently proposed MCM, and less frequently discussed models such as emulation theory, forward models, and embodiment theories. With respect to the results, it is discussed whether any of the existing theories offer a sufficient explanation for the patterns of brain activity observed during imagery, or whether there is a need for updated or new models/theories.

A total of 31 healthy participants completed a single experimental session consisting of a motor task that required them to grip a transducer at varying forces, ranging from 10-80% of their MVC (in 10% increments). 80 trials of this task were

performed via imagery, and 80 trials were performed via overt execution. The order of these conditions was pseudorandomized between participants. A single pulse of TMS was administered at 120% RMT during each trial to elicit an MEP, the peak-to-peak amplitude of which was used as a measure of corticospinal excitability. It was hypothesized that 1) during overt execution, MEP amplitude would demonstrate a positive linear relationship with force, 2) during imagery performance MEP amplitude would be linear at low forces, but plateau as force increased, and 3) that the observed trend of MEP amplitude across force levels during imagery would demonstrate a more similar trend to the overt execution condition in the high-fidelity group compared to the low-fidelity group.

6.1 General Results

There was a significant main effect of modality on MEP amplitude, meaning that the MEP amplitude observed in the imagery condition was not the same as that observed during overt execution. While the magnitude of this effect was small (partial $\eta^2 = 0.005$), it is noted that the effect was measured on the z-transformed data to account for between-group differences in MEP amplitude. There was also a significant main effect of force on MEP amplitude, with a very large effect size (partial $\eta^2 = 0.529$), showing that MEP amplitude was not the same at each level of force that participants were tested at.

The highest order significant effect was the interaction between modality and force, showing that the mean MEP amplitude observed across forces is different in the imagery condition compared to the overt execution condition. This finding aligns with the differences observed in several previous studies (Decety et. al., 1989; Cerritelli et. al., 2000; Slifkin et. al., 2008; Park & Li, 2011). The results are comparable to previous

research by Park & Li (2011) that found imagined performance of isometric finger flexion at 10-60% of an individual's maximum isometric force resulted in increased MEP amplitude in the FDS muscle compared to a rest condition, but that the magnitude of MEP amplitude did not change across forces. Although the present study found that during imagery, MEP amplitude at 10% of an individual's maximum grip force was significantly lower than that observed at all other levels, like in work by Park & Li (2011), the present study did not observe any differences in the magnitude of MEPs between 20-60% force.

It is worth noting that the tasks were not the same; the task employed in Park & Li's experiment used a finger flexion movement, while the current study used a grip task. Additionally, the design of Park & Li's task involved participants physically performing the movement in each trial, and 8 seconds following the physical movement they performed imagery of the same movement at the same force. Such differences in study design may account for the observed differences in the outcome measure.

6.2 Main Findings

6.2.1 Hypothesis 1: MEP Amplitude during Overt Execution

Results of the study showed that during overt execution MEP amplitude increased as force increased. The finding that MEP amplitude increases across force levels is in line with previous research that has demonstrated a positive trend between MEP amplitude and force (Dai et al., 2001; van Duinen et al., 2008; Perez & Cohen, 2009; Park & Li, 2013). However, contrary to the hypothesis that MEP amplitude would demonstrate a linear trend across increasing forces, this increase began to plateau around 50% of maximum grip force. Post-hoc comparisons between the different levels of force revealed

that MEP amplitude at 10% was significantly lower than that found at 20%, which was significantly lower than 30%; however, this trend was not continuous, and there was found to be no significant difference in MEP amplitude between 50 and 60%, or between 50 and 70%. Likewise, there was no significant difference between 60 and 70%, or 60 and 80%, however mean MEP amplitude at 80% force was significantly higher than that observed at 50 and 70%.

The size principle of motor unit recruitment surmises that motor units that innervate a smaller number of muscle fibers (typically slow oxidative) are recruited first, with recruitment of larger motor units (typically fast non-oxidative) following as demand increases (Henneman & Mendell, 1981). More than a third (~ 40%) of the muscle fibres in the FDS are innervated by large motor units, which recruit larger bundles of nerve fibres and are typically the fast, nonoxidative type (Hwang et. al., 2013), which are preferentially activated during rapid, high force contractions (Lederman, 2010). The recruitment of motor units during voluntary contraction should increase as force is increased in the present study, with the recruitment of more large motor units occurring at higher forces, as more muscle fibers are required to generate the target force. However, if most or all motor units are recruited at 50% force when TMS-evoked muscle activation is combined with voluntary movement, this would result in the plateau in MEP amplitude observed in the overt execution condition. Motor unit recruitment in the hand muscles has been reported to be complete at 50% MVC, with further increases in force resulting from modulation of motor unit firing rate (i.e., 'rate-coding'; De Luca et. al., 1982; Danion et. al., 2003).

Interestingly, however, this "maxing out" of motor units was not observed in all

participants: inspecting individual data, it was found that nearly half of the participants displayed a positive, linear trend of MEP amplitude across force in the overt execution condition with no evidence of a plateau. In considering these results it is important to reflect on what drives rate-coding and how this influences MEP amplitude. Rate-coding is driven by top-down control from the cortex to the motor neuron pool (Henneman & Mendell, 1981). TMS has been shown to impact a small area (1-2 cm^3) of the cortex (Rossini et. al., 2015), thus the resulting MEP is not guaranteed to be measuring the excitability of all cortical neurons that are providing descending drive to motor units of the FDS muscle. Consequently, the resulting MEP may not be a true reflection of the corticospinal excitability during movement at any given force level, although it is unknown why this would be the case at higher forces but not low ones.

One possibility is that force generation during grip is reliant on contributions from other muscles at increased forces. The FDS is the largest extrinsic flexor of the forearm and is mainly responsible for movement of the middle phalanges of the fingers and the proximal phalanges of the wrist during flexion (Okafor & Varacallo, 2021). The FDS was chosen for this study based on its location, which is superficial compared to other long flexors, and because previous TMS research using similar types of grip tasks has measured MEPs from the same muscle. There are, however, many other muscles that could play a role in modulating grip strength, including the flexor digitorum profundis (FDP) and flexor pollicis longus (FPL), which have been shown to contribute to wrist flexion and grip force production (Ambike et. al., 2013; 2014). The observed plateau at 50% force may result from the FDS muscle no longer providing further contributions to force production beyond that level.

It is also possible that in several participants, the action of gripping at higher forces was more familiar than it was to others. Many fMRI studies have shown that when performing novel tasks there is more widespread, bilateral activation of the cortices, while once a task is practiced and learned activations become more lateralized and focused in certain regions (Doyon et. al., 2003; Floyer-Lea & Matthews, 2005; Kraeutner et. al., 2018). If some participants relied on widespread, bilateral cortical activation to drive rate-coding during the higher force versions of the movement, this may explain the difference in scaling of MEPs across forces between participants in the overt condition.

There is one previously conducted study that measured MEP amplitude in the FDS muscle during finger flexion at varying forces and observed a continuously positive linear trend of MEP amplitude across 10-60% forces (Park & Li, 2013), however other research has observed the same MEP amplitude peak at 50% force in the FDS as was observed presently, with an overall U-shaped trend seen between 10-90% forces (Danion et. al., 2003; Figure 12).

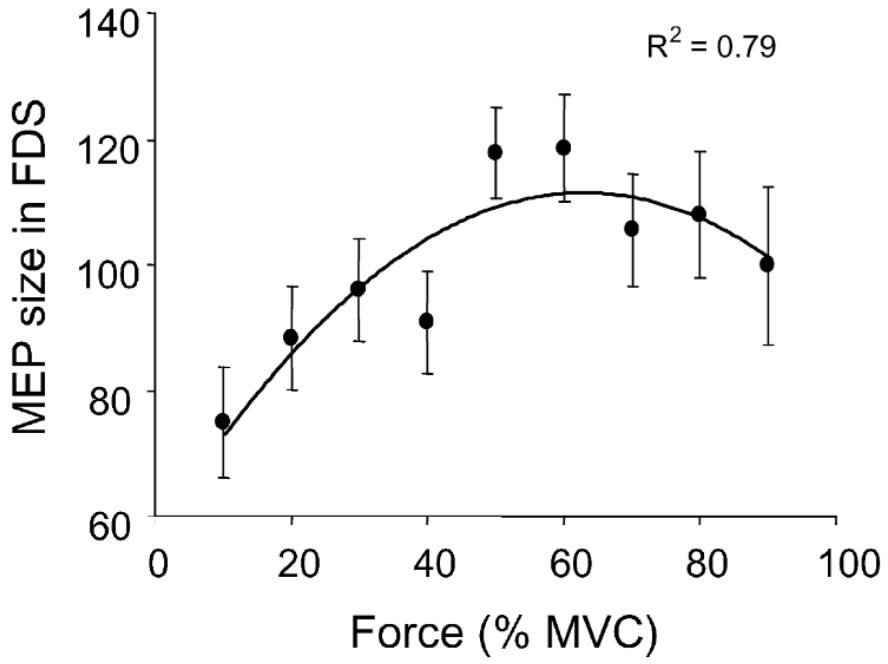

Figure 12. Quadratic Trend of MEP Amplitude in FDS. A figure from Danion et. al.'s 2003 study on MEP amplitude in the FDS muscle during contractions at varying percentages of MVC shows a quadratic trend as force is increased from 10-90% MVC.

Another possible explanation for the observed plateau in MEP amplitude during overt execution is that hemispheric activation during voluntary force generation may be dominant on the ipsilateral side at increased forces (Andrushko et. al., 2021). Approximately 90% of the fibers of the descending corticospinal tract decussate at the medulla, resulting in contralateral control, while the remaining 10% descend on the ipsilateral side (Amaral, 2000). In an fMRI study that utilized a grip task at varying percentages of participants' maximum voluntary contraction (a task identical to that which was employed in the current study), results suggested that during voluntary movement at 50 and 75% MVC, the ipsilateral M1 displayed greater activation compared to 25% MVC, which primarily demonstrated activation in M1 in the contralateral hemisphere (Andrushko et. al., 2021). Furthermore, scaling of cortical activation was not

observed in the contralateral M1 across the varying forces, whereas scaling was observed in the ipsilateral M1, such that there was significantly greater activation at 75% force compared to 50 and 25% (Andrushko et. al., 2021).

It is possible that in the present study, particularly in participants for whom the task was more novel and thus may have resulted in more widespread, bilateral patterns of brain activation, forces above 50% did not result in further activation of the contralateral M1 and instead relied on activation of networks in the ipsilateral hemisphere, the excitability of which was not measured. This would explain why the plateau in corticospinal excitability was observed around 50% force in some participants. The participants who demonstrated a linear increase in corticospinal excitability across all forces with no evident plateau (n = 15), may have had more familiarity with higher force gripping movements, and thus their brain activations during overt execution would likely have resulted in more lateralized activations, explaining the continuous increase in MEP amplitude across forces. Additionally, as noted in section 2.2.2, MEP amplitude is subject to a high degree of between-participant variability (Rossini et. al., 2015); this may explain the range of trends observed in scaling of MEP amplitude across forces between participants.

6.2.2 Hypothesis 2: MEP Amplitude during Imagery

During imagery, MEP amplitude was found to increase as force increased. Contrary to hypothesis two, the increase in MEP amplitude did not plateau at any point but demonstrated a positive trend across levels of force. Post-hoc comparisons showed that there was a significant difference between the mean MEP amplitude at 10% force compared to all other levels. There was a significant difference between the mean MEP

amplitude at 20, 30 and 40% force compared to the mean MEP amplitudes observed at 70 and 80% (but no significant differences between the former three levels), and a significant difference between the mean MEP amplitude at 50 and 60% force compared to the mean MEP amplitude at 80% (with no significant difference between the two former levels).

This finding aligns with some previous research that has demonstrated increased MEP amplitudes at higher forces (Mizuguchi et. al., 2013; Helm et. al., 2015). The insignificant differences between MEP amplitudes at the low-moderate forces (20, 30, 40, 50 & 60%) is also in line with the work done previously by Mizuguchi and colleagues, which found that there was a significant difference between MEP amplitude at 10% MVC compared to 60%, but no difference between 10 and 30% MVC, indicating that though there may be a positive correlation between MEP amplitude and force, the changes in MEP amplitude across forces are relatively small and may not be significantly different unless comparing between very high and very low forces.

6.2.3 Hypothesis 3: the Effect of Image Fidelity on MEP Amplitude

There was no main effect of order on MEP amplitude; whether participants completed the imagery block first or second, mean MEP amplitude at each force was not significantly different, meaning that contrary to hypothesis three image fidelity did not have an impact on MEP amplitude during motor imagery. This finding offered no support for the recently proposed MCM, which would predict that imagined performance of the grip task would be impacted by familiarity with the task (Glover & Baran, 2017). Unlike the previous work by Glover and Baran (2017, 2020) that involved manipulating the cognitive difficulty of a task, the current study used a task which focused on the motoric

aspects of movement, increasing the effector output required to achieve a motor goal. While it was initially considered to use some sort of cognitive manipulation to compound task difficulty (for example, a complex sequencing task like the one employed in the Van der Lubbe (2021) study that demonstrated support for the mechanisms proposed in the MCM), it was ultimately ruled out of the design of the current study in favor of a purely motoric manipulation, in order to avoid any confounds a cognitive manipulation may introduce to MEP amplitude.

In their initial paper proposing the MCM, Glover and Baran (2017) concluded that more executive functions must be involved during motor imagery performance based on a series of experiments. They tested movement duration during a reaching/grasping task performed via both overt execution and imagery and manipulated the task such that there were high and low precision conditions. They also implemented the use of a cognitive interference, argued to require the use of additional executive resources which, according to the MCM will interfere with imagery performance, specifically during novel or complex movements. Glover and Baran concluded that imagery must use additional executive resources compared to overt execution because during performance of the interference test, in which participants were required to count backwards while performing the task, movement duration in imagery was significantly slower compared to when the same task was performed with no interference. Furthermore, movement duration was significantly slower in the high compared to low precision imagery conditions when interference was added, however the interference of counting backwards had no effect during overt execution of the same task, regardless of precision.

What Glover and Baran failed to consider is whether using cognitive interference, in this instance counting backwards, is effectively changing the novelty or the complexity of the task. Separately, counting backwards and reaching/grasping are not novel skills, and though one may be unfamiliar with performing them simultaneously and it may be more cognitively difficult to imagine performing both tasks at once, on a motoric level the task is not novel nor particularly complex, and depending on one's definition of an "action", it may be argued that these experiments do not effectively test the mechanisms proposed in the MCM, specifically whether novel or complex movements require more conscious control, and therefore executive resources. In the present study, in which task difficulty was manipulated solely on a motoric level, there was no difference in corticospinal excitability in M1 during imagined movements in the high compared to low fidelity conditions, indicating that on a motoric level, image fidelity has no effect on brain excitability in the primary motor cortex during motor imagery. In terms of practical applications of imagery performance, understanding the motoric nature of imagery is essential for implementation of imagery in the fields of rehabilitation and motor training.

Though these findings may not support the mechanisms proposed in the MCM, they are also not wholly consistent with those proposed in the FEM or MST, considering that the overall trend of MEP amplitude observed during imagery was not equivalent to that observed during overt execution. The results do not oppose the idea that forward models may be implemented during imagery performance to predict the goals and consequences of an action. Forward models are purported to mimic the causal flow of an action by predicting its next state given the current state and the motor command (Wolpert et. al., 1995). Since the forward model is reliant on internal feedback, the

outcome of an action can be estimated and used even in the absence of sensory information, as is the case during imagery performance (Gerdes & Happee, 1994; Desmurget & Grafton, 2000). It is possible that the positive, linear trend observed across forces in the present study occurred because forward models implemented during imagery performance anticipated greater sensory feedback (i.e., a harder grip) on the transducer as force increased. While overall the findings of this study seem to generate more support for a model like emulation theory as opposed to the MCM, FEM, or MST, no conclusions can be made regarding forward models as the methods used in this study do not allow for an assessment of sensory feedback/sensory consequences during performance of the task. Future research should explore whether this could be incorporated into a study design to test the theories of forward models as they relate to imagery performance.

6.3 Implications for Theories

The purpose of the current research was to determine whether the findings presented evidence that a functional equivalence exists between imagined and performed movements, as stated in the popular MST and FEM theories, or whether the patterns of corticospinal excitability between these two modalities may be better explained by alternative models, such as the MCM. The results of this study did not provide any support to the mechanisms proposed in the MCM, with no effect of fidelity on MEP amplitude during imagery. While the results did not directly support the notion that imagery and overt execution are equivalent, with different trends observed across forces in each modality, the results do lend support to the idea that forward models, such as those prosed to occur in emulation theory (Grush, 2004), may drive the prediction of

action outcomes in the absence of physical movement and promote motor learning via imagery.

The FEM and MST both propose that motor imagery is a state during which a physical movement is mentally simulated. While it has been established that during motor imagery MEP amplitude is lower than during physical movement (Stinear & Byblow, 2003), the FEM and MST propose that the overall trend observed in MEP amplitude across forces in the current study should be mirrored in imagery and overt performance, which was not observed in the data. There was a significant interaction between modality and force, showing that the standardized mean MEP amplitudes across forces were different in the imagery condition when compared to the overt execution condition. Visual inspection of the data also shows that the trend across forces is not the same in imagery compared to overt execution. Post-hoc comparisons between mean MEP amplitude at each force in the imagery and overt execution conditions revealed that the differences across forces are not the same between modalities, with the imagery condition demonstrating significantly lower MEPs at low compared to high forces, but no differences between any levels of force falling between 20-60%. Conversely, in the overt execution condition MEP amplitude significantly increased from 10-50% force but plateaued thereafter.

The mechanisms proposed in MST are vague and subsequently in many studies, individual researchers are at liberty to interpret their findings in such a way that can provide support for this theory. A zealous supporter of the FEM and MST could interpret the findings of the present study as supporting these models; indeed, there is a positive, linear trend observed in the imagery condition that aligns with previous research that has

found the same trends observed across forces during overt execution in various hand muscles (Dai et al., 2001; van Duinen et al., 2008; Perez & Cohen, 2009; Park & Li, 2013). However, the trend of MEP amplitude across forces during overt execution was not found to be linear in the FDS muscle, and similar results have been demonstrated previously (Danion et. al., 2003). Whether the observed plateau at 50% force was due to saturation of motor unit recruitment or a result of preferential activation of the ipsilateral M1, if there were truly a functional equivalence between imagery and overt execution, the trends observed between 10-50% forces in the imagery condition should mimic those seen in the overt condition, which is not the case.

While the findings do not provide unambiguous support for a functional equivalence between imagined and overt performance, the observed trend of MEP amplitude across forces during imagery does not support the mechanisms proposed in the MCM either. According to this model, because conscious control must be used to monitor the unfolding image, during imagined movements attention must be switched between the motor image and the action that is being simulated. During imagined performance of a well-known simple action diverting attentional processes may be easy, however, complex or novel actions require more control, and this leads to differences between imagined and overt movements (Glover & Baran, 2017). Based on this model, it was hypothesized that MEP amplitude would demonstrate a similar pattern at low forces as was seen during overt movement, but plateau as force increased and the cognitive control required to imagine completing the task required more attention. One explanation for why this was not observed may be that manipulating force does not change task complexity on a motoric level. While it may require more physical effort to

grip the transducer at increasingly higher forces, the motor components involved in the action don't change as force increases, and consequently imagined performance of the task may not vary in complexity across forces. Additionally, while the specific task may have been novel, the general movement of gripping is a commonly performed action that was not novel to any participants. Considering this it is possible that the experimental task was simple and well-known enough that participants could easily perform imagery at all force levels, and this may explain why a relatively linear relationship was observed between MEP amplitude across forces in the imagery condition.

Previous research has found that the prediction of sensory feedback during imagery can be explained by forward models, and that the prediction of sensory feedback is consistently anticipated during imagery at varying forces (Kilteni et. al., 2018). Another possible explanation for the observed results is that during imagined performance of the grip task, forward models predict the action outcome and the sensory feedback of the motor command (i.e., gripping), and this results in an increase in corticospinal excitability that is observed at all forces, however it does not greatly differ in magnitude across forces because the action outcome and sensory feedback are more or less the same regardless of the effector output. Again, this may be a result of the chosen task being too simple in complexity; future research should consider alternate tasks that may be motorically more difficult than a hand grip motion.

6.4 Implications for Rehabilitation & Clinical Use

As previously discussed, there is conflicting evidence as to whether imagery practice is an effective tool for neurorehabilitation. Some research has concluded that imagery in addition to other therapies may improve functional outcomes in stroke

patients (Barclay et. al., 2020), however the evidence supporting the use of imagery practice on its own is inconclusive in determining whether motor imagery can drive plasticity and learning in the complete absence of physical practice.

The results of the current study provide insight into how effective imagery practice may be not only in the absence of physical performance, but in the imagined performance of a novel task. While imagery alone may not result in increased corticospinal excitability of the same magnitude as is observed during overt execution, the findings of the current research indicate that familiarity with a task may not be needed to achieve increased corticospinal excitability during imagery performance, especially if the motor task is simple and implements the use of well-known action components. Furthermore, the results of the current study indicate that on a purely motoric level, the difficulty of the imagined movement may not have a great impact on corticospinal excitability unless the movement is either very easy or very difficult.

6.5 Limitations/Future Directions

The plateau observed during overt execution was not predicted but does align with previous research that has found during overt execution motor unit recruitment in the FDS muscle is complete at 50% force, and MEP amplitude peaks at this level (De Luca et. al., 1982; Danion et. al., 2003). It is possible that in an effort to test more levels of force than had been tested in previous imagery research, the present study achieved saturation of motor unit recruitment in the FDS muscle during physical performance of the grip task in several participants when stimulating M1 during trials above 50% force. Alternatively, recent research suggests that this finding may have been due to preferential

activation of M1 in the ipsilateral hemisphere at higher forces, which would not have been detected in stimulating the contralateral M1 (Andrushko et. al., 2020).

It would be interesting for future research to explore whether the increased activation observed in the ipsilateral M1 during functional imaging could be replicated in a TMS study, showing an increase in corticospinal excitability in the ipsilateral M1 during high force movements. If so, future research should explore how corticospinal excitability changes across forces in the ipsilateral M1 during imagery performance, and whether the observed trends differ from those seen in the contralateral M1. It would also be interesting to explore whether differential corticospinal excitability is observed in the contralateral and ipsilateral M1 in individuals who are very experienced with modulating their grip strength (for example, weightlifters) compared to individuals who have less experience with the movement. Future research should also record background EMG activity from a variety of muscles, including the FDP, FPL, and possibly the abductor pollicis brevis (APB) and extensor digitorum communis (EDC). This would allow for an assessment of the contributions of other muscles to force production during grip and potentially offer an explanation for the differences in trends of MEP amplitude observed during overt execution in the present study.

To complete the analysis and compare between conditions, a z-score transformation was used to standardize MEP means around zero. In the raw data, however, there was a large difference in magnitude of MEPs in the overt execution condition compared to imagery. While this is expected based on previous literature (Stinear & Byblow, 2003), it is important to consider that during overt execution there are several external factors that influence the movement, such as sensory feedback, and these

factors could affect excitability at the spinal level and therefore amplitude of the resulting MEP (Palmieri et. al., 2004). Conversely, during imagined execution of movements, there is evidence that overt execution is actively inhibited (Blasi et. al., 2006), and therefore changes in corticospinal excitability are mainly attributable to changes at the cortical level, with less influence from changes in spinal-level excitability. Without a direct measure of spinal-level excitability, such as changes in the H-reflex, it is noted that the difference between overt and imagined performance in terms of spinal-level contributions to changes in MEP amplitude is a limiting factor in comparing between these modalities.

The present study sought to determine MEP amplitude at varying forces during imagery performance compared to overt performance of a grip task. In using TMS to elicit MEPs during physical movement, it was difficult to choose a motor task in which "effort" could be increased while the participants head could remain still enough for accurate stimulation via the coil. The choice to manipulate force during grip allowed for the task to be altered in both the imagery and overt execution conditions while ensuring that MEP measurements were accurate at all levels of the dependent variable. Additionally, it was thought that the grip task would be familiar enough that no participants would be unable to perform imagery of the task without having physically performed it first, and at the same time novel enough that no participants should be familiar with gripping at specific percentages of force relative to their maximum voluntary contraction. As discussed, however, on a motoric level the action components required to complete the grip task at 10% force do not differ from those required to complete the task at 80% force. Consequently, the task may not be complex enough, and

furthermore the grip action may be too mechanistically familiar to allow us to test the mechanisms proposed in the MCM. More research is required to determine whether the same results are observed with more complex and/or truly novel tasks.

Similarly, another limitation to consider is the difference between percentages of MVC. For each participant, the different force levels were determined based on their maximum force generated; therefore, stronger participants would have larger discrepancies between force levels, whereas participants with weaker grip strength would have much smaller differences between force. It is possible that from participant's perspectives, especially during the imagery condition where no feedback was provided, participants struggled to imagine the difference between adjacent force levels (for example, the difference between 20% and 30%, or the difference between 50% and 60%). Similar TMS studies conducted previously have found that when changes in target force are small (i.e., less than 50% MVC change) there is no difference in MEP amplitude during imagery (Park & Li, 2011; Mizuguchi et. al., 2013). Future imagery research may consider using larger intervals of forces and collecting more MEPs at each level, since small difference in force do not appear to significantly effect MEP amplitude during imagery.

6.6 Conclusions

This study found that contrary to the mechanisms proposed in the dominant theories of functional equivalence, corticospinal excitability during imagined performance of a grip task at varying forces does not demonstrate the same trend observed during overt performance of the task. The hypothesis that the observed differences between imagery and overt execution may be explained by task fidelity

during imagery practice was not confirmed by the study results, which showed no difference in corticospinal excitability between the high-fidelity imagery group compared to the low-fidelity imagery group.

Ultimately the results of this research do not provide overwhelming support for any of the current models/theories used to explain the mechanisms of motor imagery. While there may be some functional similarities between imagery and overt execution, the evidence does not support the notion that they are wholly equivalent, though forward models may be involved in the prediction of simulated action consequences. Likewise, the mechanisms proposed in the MCM are not supported by the results of the current study, with an increase in task familiarity (and consequently an increase in image fidelity) not leading to increased corticospinal excitability during motor imagery. One interpretation of this finding could be that, as discussed in the limitations, the chosen task was simply not complex/novel enough to test the mechanisms proposed in the MCM. It is also possible that motor imagery performance in general results in increased corticospinal excitability but that this increase is relatively static regardless of the task type, complexity, and novelty.

Overall, the current study has demonstrated the weaknesses of existing imagery theories and validated the need for further adaptation of these models, or perhaps even the genesis of new ones. Several avenues for future exploration have been identified and should be pursued to further our understanding of the mechanisms involved in motor imagery performance, and the parameters with which to properly utilize imagery as a tool for motor learning and rehabilitation.

Appendix A: Kiesthetic Visual Imagery Questionnaire (KVIQ)

Quantifying Imagined Movement in Non-Disabled and Pathological Systems

Participant Information			
Participant Code: _____		**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				

Appendix B: TMS Screening Form

Version: August 2021

LABORATORY FOR BRAIN RECOVERY AND FUNCTION
SCHOOL OF PHYSIOTHERAPY
DALHOUSIE UNIVERSITY
Inspiring Minds

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?		
8. Have you ever had a fainting spell or syncope (loss of consciousness)? **If yes, please describe on which occasion:**		
9. Have you ever had a head trauma that was diagnosed as a concussion or was associated with a loss of consciousness?		

10. Are you taking any medications? (please list):		
11. Do you have metal in the brain, skull or elsewhere in your body? (e.g., splinters, fragments, clips, etc.)? If so, please specify:		
12. Did you ever undergo TMS in the past? If yes, were there any problems:		
13. Did you ever undergo MRI in the past? If yes, were there any problems:		

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 C: Consent Form

DALHOUSIE UNIVERSITY

CONSENT FORM

Project title: Investigating the effect of manipulating effector load on corticospinal excitability during motor imagery

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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, you meet the study requirements, and you are free of any brain injury or disease and meet the inclusion criteria for the study.

Purpose and Outline of the Research Study
Motor imagery, the mental simulation of a movement, is thought to be a process similar to that of actual movement. Some of the evidence supporting the similarity between motor imagery and actual movement is that the time needed to imagine or perform a movement are the same. This finding appears to be true when the movements being imagined or performed are simple. When more complex or effortful movements are used, the time required to imagine the movement is longer than when the movement is actually performed. While the time needed to imagine or perform a movement is a good measure, it does not provide any information about the brain processes related to imagining these more complex or effortful movements.

The purpose of the current study is to examine the brain processes in MI when performing more complex or effortful movements, compared to those occurring during actual movement.

Who Can Take Part in the Research Study
You may participate in this study if you are over the age of 18, with 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).

KVIQ
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. 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.

Force Grip Task

The force grip task in this study will last 35 minutes. In this task you will perform a maximal grip (i.e. grip the force dynamometer (a device used to measure force) as hard as possible) three times to determine the levels of force used for the rest of the task. You will then complete two blocks of force grips, one where you imagine gripping the force dynamometer (motor imagery) and the other where you actually grip the force dynamometer. During the movement trials you will physically be grabbing the force dynamometer on each trial and in the motor imagery block you will be asked to picture the desired movement as though you are actually performing it (i.e., from "behind your own eyes"). Each block will contain 80 trials where you will be asked to align a meter on a monitor (directly in front of you) with the target force on the screen. The target box indicates a percentage of your maximal grip force (either 10,20,30, 40,50, 60,70 or 80%) and the filling of the meter relates directly to how hard you grip the force dynamometer.

During the experiment you will be seated comfortably in a chair with one hand resting on your lap and the other holding the force dynamometer. You will be provided with 2 minutes of rest every 20 trials, and four minutes of rest in between each block. During each trial, we will use 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. 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 cause 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 world-wide. 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 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 behavioral 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 $20, 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 points for the single, 120-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 de-identified 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.

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 no longer be withdrawn from the study, as this data is automatically added to the database and entered into the analysis.

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 # 2019-4871).

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 manipulating effector load on corticospinal excitability during motor imagery

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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.

_____	_____	_____
Name of Participant	Signature of Participant	Date
_____	_____	_____
Name of Investigator	Signature of Investigator	Date

Appendix D: Full Session Instruction Script

We are compensating you 20 dollars for participating in our study

Consent script

Thank you for participating in this study. Before we begin, I will give you a brief overview of the study, why it's important, and what you will be doing today.

For this study, we are interested in looking at Motor Imagery. Motor imagery is mental rehearsal of movement, and it is used in sports alongside physical practice to improve motor skills. It's also used in rehabilitation post-stroke to promote the recovery of physical ability. Currently, we do not know exactly how the parts of the brain which are required to perform motor imagery differ from those required for physical movement. However, evidence suggests that although these two processes share similarities, they are not the same. Therefore, this study aims to provide further evidence on the mechanisms of motor imagery, and how they may differ from physical movement at varying degrees of effort. Specifically, we will be comparing brain activity during motor imagery of a grip force task at varying efforts to brain activity during overt execution of the same task.

Before we get started with the experiment, we will start with a quick form. This is a screening form that we sent you via email. Once we are finished with that, we will get you set up in the TMS machine. TMS stands for Transcranial Magnetic Stimulation, and it is used to deliver brief magnetic pulses to a very specific area on your brain. By doing this, we can 'turn up' or 'down' the activity of your brain for a short period of time, and there are no permanent changes to your brain from using TMS. I'll explain the procedure once we get to the TMS machine, but basically, you will be seated on a chair with tracking glasses that will track your head placement. There will also be some electrodes, which are small stickers, placed on your arm and elbow to monitor your muscle activity.

We will spend the first 30-60 minutes getting you set up for TMS and "hotspotting", which is where we locate the area of your brain we will stimulate throughout the experiment. The next approx. 45 minutes will consist of the grip task, which I will explain further once we have you set up in the chair. For the grip task, you will do two blocks: one motor imagery and one overt execution. Overall, the study will take about 2 hours. If you have any questions while participating, feel free to ask.

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?

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 1rd 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 **

Grip Task Script

First you will be performing a max test, which will determine your maximum voluntary contraction. This value will be used as the reference force to scale your target forces during the experimental session. For the max test you'll be gripping the transducer as hard as you can 3 times, and the average of these 3 trials will be used as your max value. When gripping the transducer please keep your upper arm straight down your side, with

your elbow bent at 90 degrees. Ensure that when you grip you are only using your grip strength; do not lean into the transducer, twist your arm, or perform any other movements in an attempt to grip harder; you are not judged based on your grip strength.

If imagery block is first:

FIRST BLOCK:
During this block, you will complete the grip task using first person imagery (i.e., you will imagine what it feels like to grip the force transducer at the target force; how the muscles in your forearm, hand and fingers tighten, the feeling of the transducer on your fingers, etc.). Each trial begins with a 3-second countdown during which the target force is displayed. You will have a 3-second countdown to prepare for the trial, following which you will imagine gripping the transducer at the target force. We ask that you please keep your eyes open while performing imagery. Imagine the display in front of you, and try to picture yourself gripping the transducer and filling the meter to the target force percentage.

During each trial we will use TMS to stimulate your muscle and record brain activity. This will occur once per trial. There are 80 trials in a block, and there will be a 2 minute break every 20 trials. Following the first block, you will get a 4 minute break, then you will participate in the second block. During the second block you will be physically gripping the transducer. You will get more instructions in the break between blocks. We ask that if you have any questions throughout the experiment you wait to ask them during one of the breaks.

SECOND BLOCK:
During this block, you will be physically gripping the force transducer. The block structure will be identical to that of the previous block, with the only difference being that you will have the visual feedback of the meter filling based on your grip. Try to fill the meter to the target percentage, and maintain this for the duration of the trial. Following TMS stimulation you may relax your grip until the next trial begins.

If overt execution block is first:

FIRST BLOCK:
During this block, you will be gripping the force transducer at randomized target forces. Each trial begins with a 3-second countdown during which the target force is displayed. You will have a 3-second countdown to prepare for the trial, following which you will grip the transducer at the target force. Try to fill the meter on the right of the screen to the target percentage, and maintain this for the duration of the trial. Following TMS stimulation you may relax your grip until the next trial begins.

During each trial we will use TMS to stimulate your muscle and record brain activity. This will occur once per trial. There are 80 trials in a block, and there will be a 2 minute break every 20 trials. Following the first block, you will get a 4 minute break, then you

will participate in the second block. During the second block you will be imagining yourself gripping the transducer, without physically moving. You will get more instructions in the break between blocks. We ask that if you have any questions throughout the experiment you wait to ask them during one of the breaks.

SECOND BLOCK:
During this block, you will complete the grip task using first person imagery (i.e., you will imagine what it feels like to grip the force transducer at the target force; how the muscles in your forearm, hand and fingers tighten, the feeling of the transducer on your fingers, etc.). The block structure will be identical to that of the previous block, with the only difference being that you will no longer receive the visual feedback of the meter filling based on your grip, because you are performing the task via imagery. We ask that you please keep your eyes open while performing imagery. Imagine the display in front of you and try to picture yourself gripping the transducer and filling the meter to the target force percentage.

Debriefing Script

The study you participated in today had two main purposes. The first thing we are interested in looking at is how brain excitability scales at varying efforts during physical performance of a task in comparison to imagined performance of the same task. This is why you completed the task using both MI and ME. We are predicting that at low efforts brain excitability will be similar between MI and ME, but that differences will occur when effort is increased. We are also exploring the effect of task fidelity on brain excitability; you completed the task via (**MI or ME**; whichever applies) first, however half of our participants will be completing the tasks in the opposite order; we predict that completing the task via ME first will result in more similar scaling of brain activity during MI at higher effort tasks. If you are interested in the results of the study you can keep updated on our lab website. If you have any questions now or after you leave don't hesitate to ask. Thank you for coming in today.

For SONA participants: Your SONA credits will be applied within 24 hours. If you do not see the credits appear by then, please contact us.

Appendix E: Supplementary Data

Table S1. Demographic Information. Demographic information from the study is shown, including participant ID, age, gender, handedness, KVIQ score, and RMT. Only the 31 participants whose data were used in the analysis are shown (participants who were dropped from the study are excluded in the demographic table)

Participant ID	Age	Gender	Handedness	KVIQ Score	RMT
P001	18	M	R	15	28
P002	20	M	R	21	38
P003	23	M	R	15	28
P005	23	F	R	22	36
P006	20	F	R	25	32
P007	23	F	R	25	30
P009	21	F	R	25	39
P010	21	F	L	22	40
P011	24	M	L	23	32
P012	24	F	R	24	41
P014	22	M	R	24	35
P015	20	F	R	25	37
P016	24	F	R	19	37
P018	24	M	R	21	37
P019	19	M	R	21	32
P020	24	M	R	19	34
P023	21	F	R	20	34
P025	19	F	R	23	31
P026	22	F	R	22	31
P027	18	F	L	25	41
P028	20	F	R	21	35
P029	24	M	R	17	41
P031	18	M	R	18	39
P032	21	F	R	21	39
P033	21	F	R	25	41
P036	20	F	R	25	32
P037	18	F	R	19	35
P039	18	M	R	23	31
P040	19	F	L	25	40
P041	23	F	R	17	31
P042	24	F	R	17	37

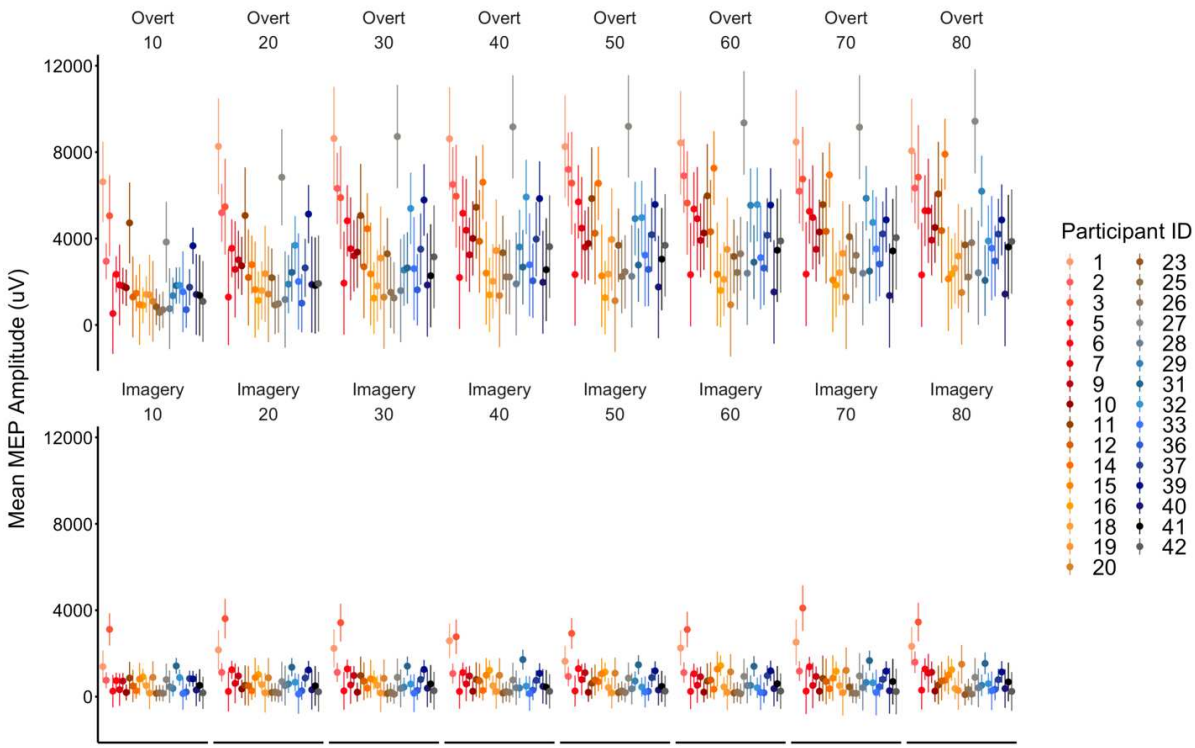

Figure S1. Raw Individual Data. Raw mean MEP amplitude is shown for each participant at each force in the motor imagery (MI; bottom) and motor execution (ME; top) conditions, where "MI 10" is the imagery condition at 10% force, etc. MEP amplitude in the ME condition demonstrated high between-subject variability. In both the MI and ME conditions there were a few participants who demonstrated consistently higher MEP amplitudes across all forces in comparison to the other participants; a visual inspection of the data from these participants was conducted to ensure that MEPs were truly higher and no outliers were skewing the data.

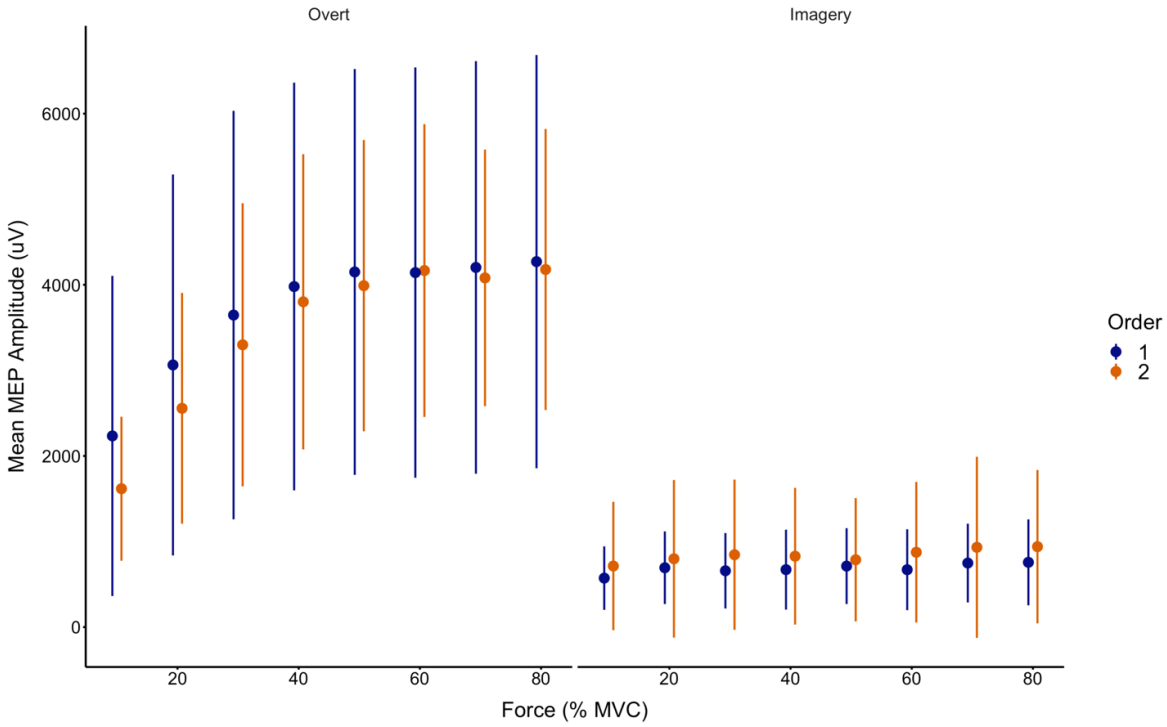

Figure S2. Raw Mean Data. Raw mean MEP amplitude is shown at each force in the motor imagery (MI; right) and motor execution (ME; left) conditions. The blue points represent data that was collected during the first block and the orange points represent data collected during the second block. As demonstrated in Figure S1, MEP amplitude in the ME condition demonstrated high between-subject variability, and homogeneity of variance is not achieved between MI and ME conditions.

```
$ANOVA
                Effect DFn DFd          SSn       SSd            F            p p<.05          ges
1          (Intercept)   1  58 3.000131e-01  2.243483  7.756136106 7.218602e-03     * 4.117880e-03
2                Order   1  58 2.166522e-04  2.243483  0.005601037 9.405995e-01       2.985984e-06
3             Modality   1  58 3.664787e-01  2.243483  9.474449000 3.179699e-03     * 5.025580e-03
5                Force   7 406 8.502189e+01 70.312703 70.133408552 5.332855e-66     * 5.395541e-01
4       Order:Modality   1  58 5.279121e-03  2.243483  0.136479335 7.131518e-01       7.275379e-05
6          Order:Force   7 406 5.307577e-01 70.312703  0.437814834 8.782675e-01       7.262004e-03
7       Modality:Force   7 406 4.137919e+01 70.312703 34.133133392 2.437289e-37     * 3.631812e-01
8 Order:Modality:Force   7 406 1.485614e+00 70.312703  1.225462578 2.873137e-01       2.006453e-02

$`Mauchly's Test for Sphericity`
                Effect         W            p p<.05
5                Force 0.0795592 3.250022e-17     *
6          Order:Force 0.0795592 3.250022e-17     *
7       Modality:Force 0.0795592 3.250022e-17     *
8 Order:Modality:Force 0.0795592 3.250022e-17     *

$`Sphericity Corrections`
                Effect       GGe        p[GG] p[GG]<.05       HFe        p[HF] p[HF]<.05
5                Force 0.5460455 3.080739e-37         * 0.5893749 5.495295e-40         *
6          Order:Force 0.5460455 7.726823e-01           0.5893749 7.869873e-01
7       Modality:Force 0.5460455 1.643393e-21         * 0.5893749 5.030464e-23         *
8 Order:Modality:Force 0.5460455 3.011817e-01           0.5893749 3.003624e-01
```

Figure S3. ANOVA Output in R. Output of the ezANOVA command in the R script that shows the main effects and interactions of the between (order, modality) and within (force) group factors. Mauchly's test for sphericity results are shown, as well as the Greenhouse-Geisser corrected values reported in the data.

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