INVESTIGATING INTERNAL MODELS DURING MOTOR IMAGERY PRACTICE

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Abstract

In overt movement, internal models predict the sensory consequences and generate motor commands for desired movements. Sensory feedback updates internal models resulting in adaptation and improved performance. It's unclear if internal models update during motor imagery, the mental rehearsal of movement. To investigate this, 66 participants were exposed to a leftwards prism shift while performing actual pointing movements (physical practice; PP), imagined pointing movements (motor imagery; MI), or no pointing movements (control). We hypothesized MI would show aftereffects like PP, indicating updating of internal models. After prism exposure, PP showed significant aftereffects ($4.73^{\circ}\pm 1.56^{\circ}$), but MI and control did not ($0.34^{\circ}\pm 0.96^{\circ}$ and $0.34^{\circ}\pm 1.04^{\circ}$, respectively). PP differed significantly from MI and control. This suggests that motor imagery does not update internal models and thus is not a simulation of overt movement. Understanding the mechanisms that underlie learning through motor imagery will lead to more effective applications of motor imagery.

List of Abbreviations Used

KVIQ	Kinesthetic and visual imagery questionnaire
MI	Motor imagery
PP	Physical practice
rTMS	Repetitive transcranial magnetic stimulation
TMS	Transcranial magnetic stimulation

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Chapter 1: Introduction

Learning and adapting motor skills (motor learning and sensorimotor adaptation, respectively) to new environments is critical to navigate our ever-changing world. While overt movement may be the gold standard for motor learning and sensorimotor adaptation, there are many situations where learning and adapting motor skills would be valuable in the absence of overt movement. For example, rehabilitating motor impairments that result from brain injury. One alternative method of learning new motor skills in the absence of overt movement is motor imagery.

Motor imagery is the mental rehearsal of a movement and can drive skill acquisition in the absence of overt movement (Jeannerod, 1995). The process of acquiring and adapting motor skills through motor imagery is not well-understood. One possible process that motor imagery may use to acquire and adapt motor skills is the internal model. Internal models consist of forward models, which use sensory predictions of desired movements to guide overt movement, and inverse models which use information of the actual and desired body position to determine the motor commands needed to achieve the desired movement (Wolpert et al., 1995). Internal models can be updated to allow for movement adaptation and better performance.

Behavioural studies investigating motor imagery and internal models demonstrate that motor imagery practice both recruits (Kilteni et al., 2018) and updates (Fleury et al., 2023; Michel et al., 2013; Rannaud Monany et al., 2022) internal models. However, there are several methodological limitations to consider. For example, excluding critical comparison groups (i.e., a physical practice group that demonstrates the true effect), using small, underpowered samples (i.e., n < 10), or having limited numbers of trials. As such,

further research is needed to solidify the concept of updating internal models during motor imagery practice. One possible method to investigate motor imagery and updating internal models is prism adaptation.

The prism adaptation paradigm involves participants reaching and pointing to a target while exposed to the prism environment – an artificial lateral visual shift (i.e., shifting everything in the visual field 15 degrees to the left). If participants can adapt to the prism environment, then they will physically reach and point in the opposite direction of the prism shift (i.e., rightwards), demonstrating aftereffects. Aftereffects represent updating internal models to the new prism environment (Prablanc et al., 2020).

The primary objective of the proposed research is to determine if motor imagery practice updates internal models using prism adaptation and a reach and point task. To accomplish this, we employed a between-subjects design of three groups – physical practice (PP), motor imagery (MI), and control. While exposed to the prism environment, the PP group physically practiced reaching and pointing to a circular target, the MI group were asked to imagine what it would look like and feel like to reach and point to the target and the control group performed an unrelated task. If motor imagery practice updates internal models, then we hypothesized that we would observe aftereffects in the MI group, like that of the PP group, and unlike that of the control group.

The findings from this research will benefit scientists interested in motor learning by deepening our understanding of motor learning and adaptation through motor imagery practice. Further, this research will provide a theoretical backbone for doctors, physiotherapists, rehabilitation specialists and even high-performance athletes who use motor imagery techniques as part of their practice.

Chapter 2: Background and Rationale

2.1 Relevance

Acquiring motor skills is a fundamental component of life. These motor skills can include performing activities of daily living such as showering and brushing one's teeth, performing occupational tasks such as typing and manual labour, and/or performing athletic endeavours such as running and throwing. **Motor learning** is necessary to acquire motor skills and is defined as the experience-dependent process of acquiring and refining motor skills, resulting in improved performance (Bastian, 2008; Krakauer et al., 2019). Learning new motor skills occurs throughout one's lifespan and is especially relevant in rehabilitation. Re-acquiring skills is a primary objective for rehabilitating brain injuries that lead to motor impairments, such as stroke (Krakauer, 2006). Given the importance of motor skill acquisition in everyday life, sport, and rehabilitation, it is important to understand the processes involved with motor learning. Some of the first researchers to define the process of motor learning were Fitts and Posner in 1967.

2.2 Theories of Motor Learning and Motor Control

In Fitts and Posner's classic theory, the process of motor learning is broken down into three stages: (1) the cognitive stage, (2) the associative stage, and (3) the autonomous stage (Fitts & Posner, 1967). To best describe these stages, examples from the sport of boxing are provided. The **cognitive stage** involves determining movement goals; this can include learning feet placement for a stable base or arm placement for protection and offense. Individuals must use a lot of cognitive resources to learn and understand components of a new skill, but they will also see quick gains in performance. The second stage is the **associative stage**, involving coordination of a movement sequence; this can

include learning a coordinated punching sequence, such as a jab, cross, and hook. Movements will feel more fluid, and individuals will notice further increases in performance. The last stage is the **autonomous stage**, where movements become an automatic process; this may include defending against a punch (jab) by moving one's head out of the way (slip) and reflexively countering with another punch (hook). Individuals require low cognitive effort to execute these movements. Ultimately, Fitts and Posner's (1967) classic theory nicely summarizes the process of motor learning into three simple stages. The following 10 years of **motor control** research, encompassing motor learning processes, motor planning, and motor execution (Schmidt et al., 2018), led to the development of further theories that guide our understanding of skill acquisition today. These theories include closed-loop control (Adams, 1971), motor programs (Keele, 1968), and schema theory (Schmidt, 1975).

Adams' closed-loop control theory (1971) suggests that learning occurs through refining perceptual-motor feedback loops. Individuals with little experience with a task, such as hitting a bullseye with a dart, will perform the movement poorly. The sensory feedback from such movement updates the motor command, thus reducing errors on further attempts. As individuals improve task performance through practice, they develop a "perceptual trace", which is used as a reference condition to compare actual movement outcomes to. According to Adams (1971), developing these perceptual traces reflects learning. One problem with Adams' theory is that closed-loop control suggests that learning exclusively occurs through feedback loops. However, individuals can perform movements effectively without visual or proprioceptive feedback. To address this issue, Keele suggested a new theory of learning through motor programs.

Keele's theory of motor programs (1968) suggests that the central nervous system organizes sequences of behaviour prior to movement initiation. Specifically, a **motor program** is a set of organized and sequenced muscle commands that are established prior to overt movement, allowing for full motor sequences to be carried out without sensory feedback. While this theory addressed the problem with Adam's closed loop theory, it is not without its faults. The primary concern of Keele's motor program theory is the question of storage for motor programs in the central nervous system. How can the central nervous system store every combination of movement patterns for every muscle in the human body? Arising from these concerns, Schmidt proposed a new theory – the schema theory – to loosen the rigidity of motor programs.

Schmidt's schema theory (1975) involves motor schemas and generalized motor programs. **Motor schemas** are memory representations of sensory consequences and parameters of movements. **Generalized motor programs** contain features that are shared by various movements such as order and phasing of events and relative force needed to execute these events. The combination of motor schemas and generalized motor programs accounts for endless movement variability while still being mindful of storage. Rather than having motor programs for every possible movement combination stored in the central nervous system, only core movement programs shared by many movements (generalized motor programs) are stored and can be adjusted with schemas. Ultimately, Schmidt's, Keele's, Adams', and Fitts and Posner's theories provide the theoretical foundation needed to understand motor skill acquisition. However, learning new motor skills, such as walking, is not enough to overcome changes in the environment or body that can occur when executing the skill, like needing to step over an exposed tree root or having sudden ankle

pain. As such, it is critical to understand how to adapt motor skills to the ever-changing environment.

2.3 Sensorimotor Adaptation and Internal Models

Sensorimotor adaptation refers to modifying the execution of current actions or selecting alternative well-practiced movements in response to a change in the environment or body (Bastian, 2008; Krakauer et al., 2019). Motor learning and motor adaptation are two distinct processes where motor adaptation adjusts already built motor plans and motor learning builds motor plans. Despite the distinction between motor adaptation and motor learning, both are necessary for motor control.

Like Adams' closed loop theory, motor adaptation relies on **error-based learning**. If one were to pick up what they thought was an empty water bottle, but was actually a full of water, the weight of the full water bottle would perturb their movement – that is, the force generated to lift the empty water bottle would be insufficient to lift the full bottle, resulting in the perturbation. In motor adaptation, the central nervous system acknowledges the perturbation through sensory feedback (in this case proprioceptive) and makes corrections to the motor command, reducing error with every lift. Thus, the central nervous system is reliant on sensory feedback to initiate adaptation. This important signal is called the **sensorimotor prediction error**, defined as the difference between actual movement outcome and predicted movement outcome (Tseng et al., 2007). Sensorimotor prediction errors allow for sensorimotor adaptation through the process of updating **internal models**.

Two models make up the internal model: the inverse model and the forward model (Wolpert et al., 1995). The **inverse model** uses information of actual and desired body position to determine the motor commands needed to achieve the desired movement

trajectory (Figure 1). The **forward model** uses sensory predictions of the desired movement to guide overt movement without sensory feedback (Figure 1). Specifically, a copy of the motor command, called the efference copy, is sent to the forward model, and used to make sensory predictions about the desired movement. At the terminus of the movement, the sensorimotor prediction error updates the forward model, allowing for movement adaptation and better performance (Wolpert et al., 1995). **Online motor control** (the control of movement during its execution) relies on inverse and forward models for smooth movement control. Overall, the internal model is responsible for making the sensory predictions about movements and updating the predictions according to sensory information and the desired movement outcome. One of the key neural regions implicated in sensorimotor prediction errors, internal models and consequently sensorimotor adaptation is the cerebellum.



Figure 1. Internal models. The inverse model gets inputs from the current state of the body and the desired state of the body to choose the desired motor commands to send to the motor system (Miall & Wolpert, 1996). A copy of the motor command is sent to the forward model to make sensory predictions about the movement which is then compared with the delayed feedback at the movement terminus.

2.4 Neural Correlates of Sensorimotor Adaptation

A large role of the cerebellum is to acquire and maintain internal models needed for sensorimotor adaptation and online motor control (Miall & Wolpert, 1996; Wolpert et al., 1998). Lesion studies and transcranial magnetic stimulation (TMS) studies are important for understanding the role of the cerebellum in sensorimotor adaptation. TMS is a noninvasive device that can transiently disrupt the activity of specific brain regions by producing a magnetic field which induces an electric current in the brain (Hallett, 2007). Repetitive TMS (rTMS) is one specific type of TMS that disrupts neural activity. When rTMS is applied to the cerebellum during sensorimotor adaptation tasks it disrupts activity in the cerebellum, providing valuable information of the role the cerebellum plays during sensorimotor adaptation.

Lesion studies report impairment to sensorimotor adaptation in the presence of cerebellar damage. In one study, Maschke and colleagues (2004) explored the influence of hereditary cerebellar ataxia during a forcefield adaptation task involving goal-directed arm movements. The experiment involved holding a manipulandum and pointing to various targets on a computer screen (see Figure 2A and 2B), comparing the performance between patients with cerebellar ataxia and healthy controls. The protocol began with one block of 120 baseline trials to familiarize the participants with the goal-directed arm movement task with no external force. Next, participants completed three blocks of 120 adaptation trials (adaptation, generalization, and retention) where they did the same goal-directed arm movements but with a force applied to the arm causing a physical perturbation. During these three blocks, trials without any external force were dispersed every 10 trials. These "catch" trials were used to evaluate aftereffects. In a forcefield adaptation task, **aftereffects**

represent evidence of updating the internal model or effective sensorimotor adaptation to the forcefield condition. Lastly, participants completed a final block of 120 trials with no external force to test generalization (see Figure 2C). Maschke and colleagues (2004) reported that cerebellar patients had impaired force adaptation, owing to a lack of aftereffects during the catch trials and generalization test block. Ultimately this study concluded that cerebellar damage leads to a failure of the cerebellum to update the internal model, resulting in impaired sensorimotor adaptation. Similar studies have also demonstrated decreased trial-by-trial performance in patients with cerebellar damage across many different movement types including walking, balancing, and eye movements (Horak & Diener, 1994; Lewis & Zee, 1993; Morton & Bastian, 2006). Further, studies on Macaque monkeys with cerebellar lesions (Baizer et al., 1999) and humans with cerebellar lesions (Weiner et al., 1983) have also demonstrated impaired adaptation to other paradigms such as prism adaptation. These lesion studies provide support for the cerebellum's critical role in internal models for sensorimotor adaptation.



Figure 2. Experimental setup and procedure. **A:** Experimental setup. The subject sat on a chair in front of the manipulandum (1) viewing the screen of a monitor (2). Both shoulders were fixed with restraints (3) to minimize forward movements of the shoulders. The monitor had a flat screen and was mounted on a desk (4) above the manipulandum. The right shoulder and handle of the manipulandum were aligned (dotted line) with the starting circle presented on the monitor and with the torque engine (5). **B:** Screenshot of targets and start area. **C:** Schema of the test conditions and their time course during the experiment (Maschke et al., 2004).

Studies using rTMS also report decreased sensorimotor adaptation following cerebellar disruption. Jenkinson and Miall (2010) used rTMS on the posterior cerebellum to evaluate its role during saccadic eye movement adaptation. Participants were divided into three experimental groups: 45% intensity, low frequency (1 Hz) rTMS; 55% intensity, low frequency rTMS; and a control group (no rTMS). Results showed a decreased ability to adapt to the saccadic eye movement task in the rTMS groups, but not the control. Additionally, as rTMS intensity increased, adaptation to the saccadic task decreased (Jenkinson & Miall, 2010). This study further demonstrates the integral role of the cerebellum in sensorimotor adaptation, specifically regarding saccadic eye movements. Further studies using rTMS to disrupt cerebellar activity demonstrate decreased sensorimotor adaptation during state estimation and adaptation tasks (Miall et al., 2007; Panouillères et al., 2012), highlighting the important role of the cerebellum in sensorimotor adaptation.

In addition to the lesion and TMS studies, Ishikawa et al. (2016) reviewed the neural substrates present in the cerebellum, providing further evidence that the cerebellum is the loci for internal models. Mossy fibers (the cortico-ponto-cerebellar projections) connect from the primary motor cortex to the cerebellum. These mossy fibers likely convey the efference copy (copy of the motor command) to the cerebellum as they fire just before movement onset. Olivo-cerebellar projections in the cerebellum are also thought to carry the error signals needed to update internal models (Ishikawa et al., 2016). These two neural projections highlight the two integral signals of the internal model: the efference copy and the sensorimotor prediction error. Ultimately, lesion studies, TMS studies, and data reviewed by Ishikawa et al. (2016) provide evidence of the cerebellum being the neural region implicated in sensorimotor adaptation.

Motor learning and sensorimotor control are important and necessary for skill acquisition and adapting learned skills to the ever-changing environment. Internal models play a critical role in sensorimotor adaptation and control, and the cerebellum is the primary loci for these internal models. Understanding the theoretical background of motor learning and sensorimotor control is of utmost importance for the field of rehabilitation, as re-acquiring skills is a prominent part of rehabilitating brain injuries that lead to motor impairment, such as stroke. However, the above sections describe skill acquisition and sensorimotor control in the context of overt movement. While overt movement may be the

gold standard for motor learning, there are many situations where learning new motor skills would be valuable in the absence of overt movement, especially in the context of rehabilitation. For instance, if a brain injury led to motor impairment resulting in the inability to move one's limbs. There are other means of skill acquisition in the absence of overt movement. One primary example is motor imagery.

2.5 Motor Imagery

Motor imagery is the mental rehearsal of a movement in the absence of overt movement (Jeannerod, 1995). It can drive skill acquisition, making it a useful tool for rehabilitating brain injuries and remediating motor impairment and dysfunction resulting from neurological disorder such as stroke (de Vries & Mulder, 2007; Zimmermann-Schlatter et al., 2008), hemiparesis (Stevens & Stoykov, 2003), Parkinson's disease (Caligiore et al., 2017), and multiple sclerosis (Agostini et al., 2021). Several theories attempt to explain how motor imagery may drive skill acquisition (for a full review see Hurst & Boe, 2022), however the process of acquiring new skills through motor imagery is not well-understood. One possible process that motor imagery may use to acquire and adapt new skills is the internal model. Motor simulation theory and motor emulation theory best implicate the use of internal models in motor imagery practice.

Motor simulation theory proposes that overt movement and motor imagery activate the same neural processes, diverging at the point of muscle activation (Jeannerod, 2001; O'Shea & Moran, 2017). This suggests that the high-level planning stages and motor plan encoding stages of overt movement are **functionally equivalent** in motor imagery practice with one distinction being that motor imagery must inhibit the muscle activation signals at a timepoint between encoding and overt action (see Figure 3). Given that motor

imagery uses the same neural processes as overt movement, theoretically motor imagery practice should use internal models for sensorimotor adaptation and control. Jeannerod (2001) claims that the motor cortex and the descending motor pathways are involved during motor imagery practice, but the exact neural processes that occur during motor imagery practice are not described in this functional equivalency model. Ultimately, motor simulation theory is broad and flexible, allowing for the assumption that motor imagery uses internal models.



Figure 3. Motor simulation theory. The stages of overt movement thought to be responsible for the experience of motor imagery are enclosed in gray (Hurst & Boe, 2022).

Since Jeannerod (2001) proposed motor simulation theory, evidence from behavioural, physiological, and neuroimaging studies further supports the functional equivalency between motor imagery and overt movement. First, behavioural studies show similar movement durations between motor imagery practice and overt movement (Decety et al., 1989; Decety & Michel, 1989; Papaxanthis, Pozzo, et al., 2002; Papaxanthis, Schieppati, et al., 2002). Second, physiological studies show changes in physiological variables such as increased heart rate with imagined movements, like that of overt movement (Decety et al., 1993, 1991). Lastly, neuroimaging studies show overlap in brain regions between motor imagery practice and overt movement, namely parietal areas, frontal motor areas, and the cerebellum (Grèzes & Decety, 2001; Hétu et al., 2013). As mentioned earlier, if motor imagery is a strict simulation of overt movement, then motor imagery practice should theoretically use the same mechanisms for making predictions about the sensorimotor consequences of actual movements. However, the exact mechanisms of internal models in motor imagery practice are not explicitly described nor explained in motor simulation theory.

An alternative and more specific theory of motor imagery-based learning that directly implicates the use of internal models is **motor emulation theory** (Grush, 2004). As mentioned earlier, the central nervous system uses forward models to make predictions about motor actions by using a copy of the motor command called the efference copy. Motor emulation theory suggests that motor imagery uses these efference copies to make predictions about the sensory consequences of movements without reliance on sensory feedback; this is defined as the "emulation process" (Grush, 2004). The **emulation process** allows for fast corrections and feedback regarding an action's force or direction without reliance on sensory input. In line with sensorimotor adaptation via internal models, motor emulation theory claims that a feedback mechanism allows for adaptation and increased accuracy of the motor emulator over time. This means that comparisons between actual sensory outcomes of an action are compared to the motor emulator's sensory predictions to adjust the motor emulator. Motor emulation theory thus suggests that motor imagery is the conscious perception of a forward model's sensory predictions.



Figure 4. Motor emulation theory. The stages of overt movement thought to be responsible for motor imagery are enclosed in gray (Hurst & Boe, 2022).

One consideration about motor emulation theory is the implementation of the motor emulator. Grush (2004) suggests that adaptation of the motor emulator occurs through a Kalman filter system. During an action, this system estimates the accuracy of the sensory input and adjusts the Kalman gain (amount of correction applied to the emulator) needed to improve accuracy of the movement. However, Grush (2004) also suggests that motor imagery practice has a Kalman gain of zero, meaning that motor imagery cannot change the emulator's predictions. This is an interesting component to Grush's (2004) theory as it suggests that only overt movement can update the sensory predictions that are used during motor imagery practice. However, some studies suggest that motor imagery practice can update these sensory predictions (Fleury et al., 2023; Michel et al., 2013; Rannaud Monany et al., 2022).

In sum, motor simulation theory and motor emulation theory provide a theoretical basis for the use of internal models in motor imagery practice. However, both theories imply that motor imagery practice makes predictions about the sensorimotor consequences of desired movements, but do not provide any experimental evidence of motor imagery doing so. The following section will describe four key papers that provide experimental support for internal models and motor imagery (Fleury et al., 2023; Kilteni et al., 2018; Michel et al., 2013; Rannaud Monany et al., 2022).

2.6 Motor Imagery and Internal Models

The concept of motor imagery using internal models is not new. Motor emulation theory speculated the use of forward models nearly two decades ago. However, experimental evidence supporting the use of internal models in motor imagery has only recently gained traction with the work of Kilteni and colleagues (2018). Prior to this study, only a single study (Michel et al. 2013) explored the topic. And since 2018, two other studies have speculated the recruitment of internal models during motor imagery practice (Fleury et al., 2023; Rannaud Monany et al., 2022). Below, each experiment is explained in detail and the section concludes with highlighting experimental limitations that must be considered when interpreting the findings.

Kilteni and colleagues (2018) were the first to investigate the computational equivalence between motor imagery and overt movement. In their study, they define **computational equivalence** as the brain's use of forward models to make predictions about the sensorimotor consequences in imagined movements being similar to that of overt movement. The experiment investigated self-generated touch: in comparison to an external touch, self-touch should produce attentuation of tactile sensations (feel less intense) because of the recruitment of forward models. Forward models are involved with predicting the sensory consequences of movements and thus can predict the expected tactile feedback for self-touch, leading to sensory attentuation of self-touch; whereas internal models are unable to make these same predictions for external touch. Kilteni et al.

(2018) observed three experimental conditions: the press condition, the imagine condition, and the base condition (Figure 5a-c). In the press condition (Figure 5b), participants pressed their right index finger against a sensor directly above their left index finger with enough force to match the external reference force felt against their left index finger. In the imagine condition, participants were asked to do the same as the press condition but rather than physically pressing the sensor they were asked to imagine themselves pressing the sensor, while still experiencing the external reference force on their left index finger (Figure 5a). In the base condition, participants were asked to relax their right hand with no physical or imagined movement (Figure 5c). In all conditions, participants were asked to report the perceived force intensity applied to the left index finger using a slider. If motor imagery is computationally equivalent to overt movement, then participants in the press condition and imagine condition should report feeling less force applied to the left index finger (sensory attenuation) compared to the base condition. The results of this study showed that both the imagine condition and the press condition showed sensory attenuation of self-touch. Thus, these findings provide evidence of a computational equivalence between motor imagery and overt movement, meaning that motor imagery practice recruits forward models to make sensory predictions about desired movements.



Figure 5. Experimental conditions. **a-c** participants received a reference force on their relaxed left index finger by a probe attached to a lever controlled by a DC motor. During the application of this reference force (3s), the participants were instructed to (i) keep their right hand and right index finger relaxed on top of a support (base; **a**); (ii) press a sensor with the right index finger (press; **b**); or (iii) imagine pressing the sensor with their right index finger (imagine; **c**). When pressing or imagining pressing, they were instructed to use as much force as they felt was required to match the reference force that they simultaneously felt on the left index finger. Immediately afterwards, they were asked to reproduce the reference force by using a slider controller the force output on their left index finger (Kilteni et al., 2018).

An earlier study also investigated the presence of internal models in motor imagery practice using prism adaptation in a two-part experiment (Michel et al., 2013). In their first experiment, 54 participants performed an arm pointing task and were divided into six experimental groups: prisms-active, prisms-imagery, prisms-stationary, prisms-stationary-attention, no prisms-imagery, and no conflict-prisms-imagery (see Table 1 for descriptions of each group). The experimental procedure involved a *pre-test* with no prism exposure (12 trials), a *test* with 15° rightward optical shift prisms (100 trials), and a *post-test* after prism exposure (12 trials). Similar to the Maschke et al. (2004) force-field adaptation paradigm described earlier, prism adaptation leads to aftereffects, the presence of which provide evidence of updating internal models to new experimental conditions. If motor imagery practice updates internal models during prism exposure, then the prisms-imagery group

should show aftereffects similar to the prisms-active group in the post-test block. The results of this first experiment were that the prisms-active and prisms-imagery groups showed aftereffects, indicating adaptation to the prism condition (Figure 6). Additionally, the magnitude of adaptation was greater in the prisms-active group compared to the prisms-imagery group. The authors suggest that the findings indicate an **intersensory realignment**, aligning the visual and proprioceptive feedback during prism exposure (a process that involves updating internal models), during motor imagery practice under the prism condition (Michel et al., 2013). These results were further supported by experiment two.

Group	Description	Wearing 15° Rightward Optical Shift Prisms (Yes/No)	Vision of Initial Hand Placement (Yes/No)
Prisms-Active	Participants physically pointed to visual targets as fast and accurately as possible.	Yes	Yes
Prisms-Imagery	Participants imagined how it would feel to point to visual targets as fast and accurately as possible without physically moving.	Yes	Yes
Prisms-Stationary	Participants remained relaxed. No movement or imagery practice. Watched the visual targets without responding.	Yes	Yes
Prisms- Stationary- Attention	Participants remained motionless and imagined linking the top of their right index finger to the visual target.	Yes	Yes
No Prisms- Imagery	Participants imagined how it would feel to point to visual targets as fast and accurately as possible without physically moving, wearing flat lenses with no visual shift.	No	Yes
No Conflict- Prisms-Imagery	Participants imagined how it would feel to point to visual targets as fast and accurately as possible without physically moving.	Yes	No

Table 1. Descriptions of each experimental group in the Michel et al. (2013) study.



Figure 6. Visuo-manual pointing errors. Pre-test (black symbols) and post-test (white symbols) pointing errors for the six experimental conditions. The mean value \pm standard error for prisms-active (PA), prisms-imagery (PI), prisms-stationary (PS), prisms-stationary-attention (PSA), no conflict-prisms-imagery (NCPI), and no prisms-imagery (NPI) conditions are shown. The stars symbolize Scheffé post-hoc significant difference. The main finding is that prism adaptation occurred in PA and PI conditions (Michel et al., 2013).

Experiment two clarified the intersensory realignment during prism adaptation and motor imagery practice. In this study, 20 new participants were divided into two experimental groups: prisms-active and prisms-imagery. The experimental procedure and description for each group remained the same as experiment one. The only difference was that during the prism condition (test block), every 10 trials involved three "open loop pointing trials" (pointing without vision trials) to assess the development of adaptation. The results of the second experiment were that both prisms-active and prisms-imagery showed a leftward shift following prism exposure. Michel et al. (2013) suggested these results further support sensory realignment during prism adaptation with motor imagery practice. Ultimately, this two-part study provides evidence of internal models being used and updated to new environmental conditions during motor imagery practice.

The next study investigating the presence and updating of internal models during motor imagery practice was published in 2022 by Rannaud Monany and colleagues. This study explored whether motor imagery practice can update internal models to a radically new environment – microgravity. The experimental protocol involved an arm swinging movement split into three testing blocks: pre (4 trials), flying time (10 trials), and post (4 trials; see Figure 7). Three experimental groups were compared: control (n = 8), exposed (n = 8), expos = 6), and imagine (n = 9). During the pre and post test blocks, all groups performed trials of physical arm swinging movements, imagined arm swinging movements, and imagined arm swinging movements where participants imagined a zero-gravity environment; times to perform each movement were recorded. During the flying time block, the control group remained on the ground and performed unrelated normal activities; the exposed group was exposed to microgravity and performed unrelated normal activities; the imagine group was exposed to microgravity and practiced the arm swinging movement using motor imagery. If motor imagery practice can update internal models to microgravity conditions, then the arm swinging movements will be slower after microgravity exposure in the imagine group but not the control and exposed groups. Results showed that the time for imagined arm swinging movements in an imagined zero-gravity condition only increased in the imagine group (Figure 8), indicating that motor imagery practice updated internal models to the microgravity environment. There were no significant increases in time for the physical or imagined arm swinging movements for the exposure group, suggesting that mere microgravity exposure is not enough to update internal models to the environmental

condition. The findings of this paper support the findings of Michel et al. (2013), providing further evidence of updating internal models during motor imagery practice.



Figure 7. Schematic representation of the experimental procedure. A_{1g} , actual movement in 1 g; I_{1g} , imagined movement in 0 g (during or not during exposure to 0 g). In the pre-testing block, all participants completed the Kinesthetic and Visual Imagery Questionnaire (KVIQ) followed by 4 trials of physical arm swinging movements and then 4 trials of imagined arm swinging movements. In the flying time block: the control group performs unrelated activities, remaining on the ground; the exposed group performs unrelated activities while exposed to 0 g; and the imagine group performs 10 imagined arm swinging movements while exposed to 0 g. In the post-testing block, all participants completed 4 imagined arm swinging movements followed by 4 physical arm swinging movements (Rannaud Monany et al., 2022).



Figure 8. Movement duration for physical and imagined arm swinging movements. For control, exposed, and imagine groups in pre- and post-tests for actual movements in 1 g (A_{1g}), imagined movement in 1 g (I_{1g}), and 0 g (I_{0g}). Vertical bars represent standard deviations. White circles represent individual observations per condition. *P < 0.005 (Rannaud Monany et al., 2022).

The final, and most recent, experiment investigating internal models and motor imagery practice was published in 2023 by Fleury and colleagues. Following the Michel et al. (2013) study on motor imagery and prism adaptation, Fleury et al. (2023) explored motor imagery, prism adaptation, and inter-task transfer. The purpose of this prism adaptation study was to observe whether after-effects produced by the prisms during motor imagery practice can be transferred between skills, specifically pointing and throwing. In accordance with the methodology of Michel et al. (2013), the study recruited 44 participants split into three experimental groups (minimum 10 per group): active, inactive, and motor imagery. The procedure started with a familiarization phase where all groups physically practiced 30 trials of throwing and six sequences of five pointing movements (see Figure 9). Pre-tests followed, where participants physically performed 20 trials of throwing and 20 pointing movements. Next was the exposure phase; participants were exposed to prism lenses that shifted their vision 10 degrees to the right and each experimental group performed slightly different tasks. The active group performed 20 sequences of five physical pointing trials (100 trials in total). The imagery group vividly imagined the pointing movement for 20 sequences of five imagined pointing trials. The inactive group passively watched their motionless hand for five minutes while answering trivial questions from the study investigator. The last phase, post-tests, involved 20 physical trials of throwing and 20 physical trials of pointing for all groups. If motor imagery updates internal models, then aftereffects should be present in the motor imagery group similar to the active group, but not in the inactive group. Further, if these aftereffects are transferable, then the motor imagery group should have significant aftereffects for both throwing and pointing in the post-tests similar to the active group, but unlike the inactive group. Results showed that the motor imagery group demonstrated significant aftereffects, but only in participants who reported high motor imagery abilities (assessed via the Movement Imagery Questionnaire). Further, participants with high motor imagery abilities demonstrated significant aftereffects for throwing movements after not previously practicing throwing during the prism exposure. However, these aftereffects were not significantly different to the inactive group. Thus, the overall findings of Fleury et al. (2023) were that participants with high motor imagery abilities experienced aftereffects, signifying the ability to update internal models with motor imagery practice. These findings agree with Michel et al. (2013) and Rannaud Monany et al. (2022), suggesting that motor imagery practice updates internal models.



Figure 9. Experimental procedure included four steps: familiarization, pre-tests, exposure, and post-tests. Visual feedback was available during familiarization and post-tests and was precluded during pre- and post-tests. During familiarization, pre-tests, and post-tests, all participants performed both tasks in a pseudo-randomized order. During exposure, participants from the active group actively performed 20 sequences of pointing while those in the imagery groups (MI+ and MI-) imagined the same sequences. Participants from the inactive group remained motionless during exposure and responded to trivial questions asked by the investigator.

There are several experimental limitations in these studies which need to be considered when interpreting the findings. First, Michel et al. (2013) and Rannaud Monany et al. (2022) excluded key experimental groups. Michel et al. (2013) did not include a *no conflict prisms-active group* (no vision of starting hand position during overt movement of reach and point task) but did include a *no conflict prisms-imagery* group. Interestingly, the *prisms-imagery group* (vision of starting hand position) had significant aftereffects and the *no conflict prisms-imagery group* (no vision of starting hand position) had non-significant aftereffects, however the authors did not elaborate on these findings. A comparison between a *no conflict prisms-active group* and a *no conflict prisms-imagery group* may provide insight on the differences observed in the two imagery groups. Rannaud Monany et al. (2022) did not include an overt movement comparison group. There was no experimental group that physically practiced the arm swinging movements while also exposed to the microgravity conditions. As such, there was no experimental group to show the expected results of updating internal models during microgravity exposure.

Second, none of the three studies (Michel et al., 2013; Rannaud Monany et al., 2022; Fleury et al., 2023) performed a priori or post-hoc power analyses, and in all three studies each experimental group had a small sample size (n \leq 10), and none reported effect sizes. Collectively, these limitations make it difficult to gauge the practical significance of the reported results. To show a significant practical effect, a larger sample is needed. For example, to measure a large effect (f = 0.8) for between group comparisons with a two-way ANOVA, a minimum of 22 participants per group is needed. Thus, more participants are needed to verify that internal models are updated during motor imagery practice.

Lastly, all studies had limited exposure trials. Michel et al. (2013) and Fleury et al. (2023) included only 100 trials during prism exposure. A recent meta-analysis on prism adaptation suggests that participants wearing 15° leftward prisms should be exposed to the condition for more than 10 minutes or about 250 trials (McIntosh et al., 2019). As such, to assume appropriate adaptation to the prism condition, more trials and exposure are needed. Rannaud Monany et al. (2022) included only 10 trials during anti-gravity exposure. Most motor imagery practice studies incorporate more trials; for example, a commonly used serial reaction time task typically involves several blocks of 250 motor imagery trials (Kraeutner, MacKenzie, et al., 2016; Solomon et al., 2021). As such, more trials are needed to ensure adaptation of the sensorimotor system.

Ultimately, the four studies described above provide evidence that internal models used in motor imagery practice. This suggests that there is a computational equivalence

between motor imagery practice and overt movement, supporting the ideas presented in motor simulation theory and motor emulation theory. However, as discussed above, there are several limitations that need to be considered. Additionally, while Kilteni et al. (2018) had few noticeable experimental limitations, the experiment itself only provided evidence of the presence of forward models during motor imagery practice and thus did not provide support for updating internal models to new environmental conditions. Thus, further research is needed to solidify the concept of updating internal models to new conditions during motor imagery practice. Adaptation paradigms can be used to explore sensorimotor adaptation and updating forward models.

2.7 Adaptation Paradigms

There are four adaptation paradigms that can investigate sensorimotor adaptation and updating internal models: forcefield adaptation, Coriolis forcefield adaptation, visuomotor rotation adaptation, and prism adaptation. Briefly, in **forcefield adaptation**, participants adapt to a forcefield manipulandum that applies forces to a participant's hand during a reaching movement (Shadmehr & Mussa-Ivaldi, 1994). In **Coriolis forcefield adaptation**, participants perform a reaching movement while seated in a rotating chair; the rotational force from the rotating chair causes a physical perturbation to the reaching movement (Coello et al., 1996; Lackner & Dizio, 1994). In **visuomotor rotation adaptation**, the participant's cursor position is coupled with the participant's index finger position; the relationship between the cursor and finger position is then perturbed by adding a rotation of the visual moving hand (Krakauer, 2009; Krakauer et al., 2000; Prablanc et al., 1975). Lastly, in **prism adaptation**, subjects wear prism lenses that shift the visual field laterally, causing a pointing error (Prablanc et al., 2020; Redding & Wallace, 1993). In all
paradigms, there is an inconsistency between the predicted sensorimotor information of the moving limb and the actual sensorimotor information, triggering error signals (Fleury et al., 2019). These error signals derive from the feedback error between the vision of the target/limb at the terminus of the movement and it's actual location (Fleury et al., 2019). The resulting measurement in these adaptation paradigms is the **aftereffect**, which reflects adapting to the new experimental condition (forcefield, Coriolis force, visuomotor rotation, or prism) via updating internal models.

One major methodological consideration for forcefield adaptation, Coriolis forcefield adaptation, and visuomotor rotation adaptation is whether the aftereffect truly represents changes in a person's sensorimotor system. The aftereffect in these adaptation paradigms may rather reflect adapting to the interface properties (such as the forcefield manipulandum) whereas adapting to prisms better reflects adaptation of the sensorimotor system (Fleury et al., 2019). Specifically, the aftereffect from prism adaptation remains the same strength when prisms are replaced by sham prisms or are removed (Fleury et al., 2019). As such, prism adaptation is the preferred adaptation paradigm to explore the presence and updating of internal models during motor imagery practice.

2.8 Prism Adaptation

Prism adaptation procedure involves pre-tests, prism exposure, and post-tests (see Prablanc et al., 2020 for detailed descriptions; Figure 10). Typically, participants perform goal-directed pointing tasks during these three testing blocks, but participants may perform alternative visuomotor tasks, such as throwing (Martin et al., 1996). **Pre-tests** involve measuring baseline performance of the goal-directed pointing task. **Prism exposure** involves wearing prism lenses that laterally shift the vision of the target (i.e., 15° leftward)

causing pointing errors in the same direction as the prismatic deviation (direct effects). **Post-tests** involve removing the prism goggles and measuring aftereffects, visuo-motor pointing errors made in the opposite direction of the prismatic deviation, indicating sensorimotor adaptation.



Figure 10. Classical prism adaptation procedure. The figure illustrates the three distinct phases: pre-tests and post-tests that are measured in open loop conditions and exposure, under closed loop conditions. The general evolution of terminal pointing errors during the three phases is plotted. Meanwhile, the figure shows the contribution of the two classically described components of prism adaptation: strategic control, accounting for rapid error reduction, and sensory realignment responsible for the presence of after-effects (Fleury, 2020).

In basic prism adaptation procedure, goal-directed pointing tasks have two conditions: open loop pointing and closed loop pointing. During **open loop pointing**,

participants do not receive visual feedback for movement trajectory and outcome, whereas

during **closed loop pointing**, participants do receive visual feedback (Prablanc et al., 2020). Participants perform open loop pointing during pre-tests and post-tests to prevent the risk of de-adaptation, and closed loop pointing during prism exposure to trigger adaptation.

The type of adaptation (sensory realignment) depends on the type of visual feedback available during closed loop pointing in prism exposure (Prablanc et al., 2020; Redding et al., 2005). **Concurrent exposure** allows visual feedback during the pointing movement and at the terminus of the movement. In some cases, researchers will provide visual feedback of the starting hand position, but not the movement trajectory. In others, researchers will provide feedback for the whole movement. **Terminal exposure** only allows visual feedback at the terminus of the movement. Vision guides proprioception during concurrent exposure, causing realignment of the proprioceptive system, while proprioception guides vision during terminal exposure causing realignment of the visual system (Redding & Wallace, 1988). While studies have demonstrated aftereffects in both terminal and concurrent exposure, the type of exposure method affects the type of aftereffects obtained (i.e., whether vision guides proprioception or proprioception guides vision)(Herlihey et al., 2012).

There are two main processes involved in prism adaptation: strategic control and sensory realignment (see Figure 10 above)(Prablanc et al., 2020; Redding et al., 2005). **Strategic control** during prism adaptation allows for fast error reduction and improved performance during initial prism exposure. It is considered the fast, learning component of prism adaptation, where learning occurs with error correction. Strategic control best describes the components of prism adaptation that are not attributed to true adaptation.

Sensory realignment during prism adaptation is the main contributor to aftereffects. It is considered the slow, "true" adaptation component of prism adaptation. This process reduces the mismatch between the proprioceptive and visual systems through sensory prediction errors that trigger adaptative changes (Prablanc et al., 2020; Redding et al., 2005). The adaptative changes that occur during sensory realignment rely on updating internal models (Fleury et al., 2019).

Several neuroimaging studies suggest the cerebellum, the neural region for internal models, as a key neural region involved in prism adaptation processes (Chapman et al., 2010; Küper et al., 2014; Luauté et al., 2009; Panico et al., 2016). In a recent review, Panico et al. (2020) investigated the neural correlates of prism adaptation and proposed an interpretive framework for prism adaptation. In this framework, the cerebellum is active from early prism exposure to presence of aftereffects. During early prism exposure, the cerebellum facilitates error processing, helping to improve performance. From early prism exposure to presence of aftereffects, the cerebellum facilitates realignment. The cerebellum's crucial role in sensorimotor control and processing sensory feedback errors allows for realignment processes. It is important to note that prism adaptation also recruits other neural regions including parietal areas and the primary motor cortex. Panico et al. (2020) suggested the cerebello-parietal network as the main network that mediates prism adaptation and realignment: the cerebellum works to recruit internal models to help with realignment; the parietal areas help with strategic adjustment of movement directions. Lastly, the primary motor cortex may help consolidate information related to aftereffects (Panico et al., 2020).

Ultimately, prism adaptation is a useful method to study sensorimotor adaptation processes. In comparison to other adaptation paradigms (forcefield adaptation, Coriolis forcefield adaptation, and visuomotor rotation adaptation), prism adaptation better reflects true adaptation processes rather than adapting to interface properties. Specifically, sensory realignment during prism adaptation is the process of true adaptation, relying on sensory prediction errors and updating internal models. This is further supported by neuroimaging studies which highlight engagement of the cerebellum, the main neural region involved with internal models, during prism adaptation processes including sensory realignment. Prism adaptation researchers can behaviourally observe adaptation and updating internal models through measuring aftereffects, and this has been done with overt movement and twice with motor imagery practice. Thus, prism adaptation is an excellent method to investigate updating of internal models during motor imagery practice.

Chapter 3: Research Questions and Hypotheses

The review of literature in Chapter 2 suggests that motor imagery practice may update internal models, and this may help with motor skill acquisition and control. However, the current motor imagery theories (motor simulation theory and motor emulation theory), suggesting the involvement of internal models, provides little supporting experimental evidence. Additionally, the current studies on this topic have several limitations including small sample sizes, a lack of appropriate experimental group comparisons, and limited numbers of trials. As such, we need a robust experiment to investigate the role of internal modelling during motor imagery practice. Understanding the nature of skill acquisition and control during motor imagery practice is crucial in disciplines where overt movement is not possible, such as re-acquiring skills during rehabilitation of brain injuries that led to motor impairments.

The current research seeks to add to our understanding of sensorimotor control and motor imagery through understanding if internal models play a role in sensorimotor adaptation during motor imagery practice. Thus, the primary objective of the current research is to investigate the updating of internal models during motor imagery using prism adaptation and a reach and point task. We hypothesize that if motor imagery updates internal models, then aftereffects will be present during motor imagery-based practice after prism exposure, similar to overt movement.

Chapter 4: Methodology

4.1 Participants

Sixty-seven healthy subjects (35 female, aged 18-64 years) agreed to participate in the study. The required sample size was determined using a power analysis with G*Power software. Previous work reported a large effect for aftereffects in prism adaptation during a physical pointing task (d = 0.95)(McIntosh et al., 2019). No previous research has reported effect sizes for prism adaptation during motor imagery practice. Thus, we approximated the sample size using a smaller, yet still large effect size of 0.8 to ensure an appropriate sample size for motor imagery practice. To have an 80% chance of detecting a large effect (f =0.40) between groups in a two-way ANOVA, we need a total of 66 participants (22 per group). Participants were recruited using the Dalhousie Undergraduate Psychology Pool (SONA), word of mouth, posters placed throughout the university community, DalNews email, and social media (see Appendix A).

All participants were over the age of 17, with normal or corrected-to-normal vision, and no self-reported neurological injury or disease that would preclude their participation. The Edinburgh Handedness Inventory was used to assess participants' handedness (Oldfield, 1971), and the Kinesthetic and Visual Imagery Questionnaire (KVIQ) was used to assess participant's imagery ability. Participants self-reported their age and sex. Ethical approval was obtained from the Dalhousie University Social Sciences and Humanities Research Ethics Board (REB # 2023-6649) and all participants were provided written, informed consent prior to their participation.

4.2 Questionnaires

4.2.1 Edinburgh Handedness Inventory

The Edinburgh Handedness Inventory is a screening tool for handedness that consists of 10 activities of daily living (Oldfield, 1971)(Appendix B). Participants were asked to report their preferred hand for each activity of daily living. A score of greater than +40 indicates right-handedness; a score of less than -40 indicates left handedness; and a score between -40 and +40 indicates ambidexterity. Scores from the Edinburgh Handedness Inventory were used to determine handedness for the experimental task. In the case of ambidexterity, participants chose their preferred hand for the experiment.

4.2.2 Kinesthetic and Visual Imagery Questionnaire

The Kinesthetic and Visual Imagery Questionnaire is a questionnaire used to assess the vividness and sensation intensity of the visual and kinesthetic dimensions of motor imagery, respectively (Malouin et al., 2007)(Appendix B). The visual and kinesthetic dimensions of motor imagery are evaluated using a self-report rating from 1 to 5. In the visual dimension, a score of 1 represents imagining no image at all and a score of 5 represents imagining an image as clear as seeing. In the kinesthetic dimension, a score of 1 represents imagining no movement sensation and a score of 5 represents imagining movements as intense as overt movement. The KVIQ has shown high reliability in both healthy controls and clinical populations (Malouin et al., 2007) and has previously been shown to be an excellent predictor of motor imagery performance (Kraeutner, Eppler, et al., 2020). The KVIQ was used to ensure that the experimental groups will not differ significantly in average imagery ability and was not used as a screening tool. Demographic information including age and sex was recorded as part of the KVIQ.

4.3 Experimental Task

Participants were seated comfortably in a chair facing a desk with a keyboard positioned at the end of the desk, nearest to the participant, and a touchscreen monitor (PCT2485 Touch LED LCD Monitor, Planar, Hillsboro, OR) placed behind the keyboard (Figure 11). The touchscreen was angled slightly towards the participant by propping up the back of the screen to improve visibility. The participants rested their non-dominant arm in their lap and placed their dominant index finger on the spacebar of the keyboard. Participants performed a custom reach and point task programmed in Python (Version 3.9.13) on the touchscreen monitor using their dominant hand. There were three trial types: physical practice, motor imagery, and control. During physical practice trials, participants pressed and held the spacebar until after a 400-600ms delay a 10 mm diameter circular target appeared randomly at one of three locations on the touchscreen monitor (centre of screen, 10% to the left of centre, 10% to the right of the centre); participants then released the spacebar and reached and pointed to the target as quickly and accurately as possible. Upon touching the screen, the target would disappear and the pixel coordinates of the location of the screen contact was recorded alongside total movement time (time from presentation of the target to screen contact). During motor imagery and control trials, participants pressed and held the spacebar until after a 400-600ms delay the target appeared randomly at one of the three locations on the touchscreen monitor. Participants kept their finger pressed on the spacebar while imagining reaching and pointing to the target (motor imagery trials) or imagining a line drawing itself straight from the center of the target to the participant's dominant index finger (control trials). When participants were finished the trial, they released the spacebar and the target disappeared from the screen, ending the trial. Total movement time in motor imagery and control trials was recorded as the time from

presentation of the target to release of the spacebar. For the motor imagery trials, participants were instructed to perform kinesthetic imagery using a first-person perspective, focusing on the sensory aspects of the reach and point task.



Figure 11. Experimental setup. A) Participant pressing the spacebar with their dominant index finger, presenting the circular target on the touchscreen tablet. B) Participant reaching and touching the target with their dominant index finger.

The experiment involved four blocks: familiarization, baseline testing, prism exposure, and final testing. During familiarization, participants completed physical practice trials while wearing goggles with clear, non-prism lenses (3MTM 47110 Over-The-Glass Impact Resistant Clear Safety Glasses, London, ON, Canada). These familiarization trials were closed loop, where participants viewed their starting hand position, movement trajectory, and terminal hand position. During baseline and final testing, participants completed physical practice trials while wearing PLATO goggles (Translucent Technologies, Toronto, ON, Canada). Participants viewed their starting hand position, but after viewing the target on the screen, the PLATO goggles closed when the participants removed their finger from the spacebar to reach for the target. This occluded the participant's vision of their movement trajectory and terminal hand position (open-loop trials). Finally, during prism exposure, participants completed either physical practice, motor imagery, or control trials. Participant wore the same clear goggles as in familiarization, but with 35 diopter prism lenses attached (The Fresnel Prism and Lens Co., Bloomington, MN). These lenses shifted the visual field 17° to the left, as per the recent meta-analysis recommendations for prism studies (McIntosh et al., 2019). These trials were closed loop, where all participants viewed their starting hand position, and participants completing physical practice trials also viewed their movement trajectory and terminal hand position (not applicable to motor imagery and control trials, as the participants' dominant finger never left the spacebar).

4.4 Experimental Protocol

Prior to the onset of the study, participants were randomly assigned to one of three experimental groups: a physical practice group (PP), a motor imagery practice group (MI), or a control group. Participants first provided written informed consent, completed the Edinburgh Handedness Inventory, and were administered the KVIQ. The investigator oriented each participant to the reach and point task prior to starting the experimental blocks. Familiarization consisted of 40 self-paced closed-loop physical practice trials over approximately three minutes. Next, participants performed the baseline testing block, consisting of 10 self-paced open-loop physical practice trials. The prism exposure block consisted of 250 self-paced closed-loop physical practice, motor imagery, or control trials (10 blocks of 25 trials) over approximately 15 minutes. Final testing consisted of 10 self-

paced open-loop physical practice trials over approximately one minute. Following this block, the experiment is complete, and all participants received a debriefing form (Appendix D). An overview of the experimental protocol is shown in Figure 12.



Figure 12. Schematic of the experimental procedure. In the familiarization block, all groups performed 40 closed-loop physical trials of the reach and point task. In the baseline block, all groups performed 10 open-loop physical trials of the same task. In the prism exposure block, the physical practice group was instructed to perform 250 closed-loop physical trials of the reach and point task; the motor imagery group was instructed to perform 250 closed-loop does loop motor imagery trials of the reach and point task; and the control group was instructed to perform 250 closed-loop control trials. In the final test block, all groups performed 10 open-loop physical trials of the reach and point task.

4.5 Data Analysis

The primary outcome measure was the magnitude of aftereffects during the final test block. Aftereffects are characterized by the distance of the participant's finger from the center of the circular target in the x (horizontal) direction, measured in mm, in the final test block. This distance is converted from mm to visual angle using the equation below.

visual angle (degrees) =
$$\tan^{-1} \left(\frac{distance from target (mm)}{distance from screen (540 mm)} \right) \times \frac{180}{\pi}$$

A two-way ANOVA was used to determine if internal models can be updated during motor imagery, as indicated by 1) the magnitude of aftereffects (between-group analysis); and 2) the presence of aftereffects (within-group analysis). The two-way ANOVA model included factors of group (PP, MI, and control) and time point (baseline and test) and the outcome variable was the average aftereffects for each group. Post-hoc analyses were used to determine significant differences between groups, time point, and the interaction of group and time point. Effect sizes were calculated to characterize the magnitude of the effect. Statistical analyses were performed using open-source statistical software 'R' (Version 4.2.2) with $\alpha = 0.05$ denoting significance.

Experimental code, data, and analysis code are openly available in the Open Science Framework repository

(https://osf.io/6tv5m/?view_only=f1a3d858c4004ffb8fc4b0b386f429ce).

Chapter 5: Results

5.1 Participants

Of the 67 participants recruited, one was excluded due a software error that precluded them from completing the experiment. Thus, 66 participants (n = 22 in the PP, MI, and control groups) were included in the analysis. Participants ranged from 18-65 years of age (Table 1), with 35 females and 3 left-handed individuals. We confirmed motor imagery ability through the KVIQ and checked compliance with performing motor imagery via total movement time during exposure trials between the MI and PP groups, assuming movement time during motor imagery trials would be as long or longer than that observed for physical practice trials (Dahm & Rieger, 2016; Guillot & Collet, 2005). The mean scores for the visual and kinesthetic components of the KVIQ (Table 1) were not significantly different amongst groups [visual: F(2,63) = 0.91, p > 0.05, $\eta^2 = 0.028$; kinesthetic: F(2,63) = 0.98, $\eta^2 = 0.030$, p > 0.05] and these values were within the previously reported range for healthy controls (Malouin et al., 2007). Further, total movement time for the motor imagery trials during prism exposure in the motor imagery group (M = 1879.97 ms, SD = 154.65 ms) was greater than zero. Further these movement times were longer, but comparable to the physical practice trials during exposure in the physical practice group (M = 677.05, SD = 28.74 ms) as literature demonstrates that time to imagine a movement is typically slower than overt execution (Dahm & Rieger, 2016; Guillot & Collet, 2005).

Group	Age		KVIQ-V		KVIQ-K	
	М	SD	М	SD	M	SD
РР	24.52	9.5	19.74	5.30	20.96	5.20
MI	29.68	11.93	20.23	4.32	20.41	4.34
Control	25.18	5.16	21.64	3.57	22.41	2.87

Table 2. Participant descriptive statistics including age and KVIQ scores.

5.2 Checking the Assumptions of a Two-Way ANOVA

Shapiro-Wilk's tests demonstrated that the visual angle scores during the baseline block for the MI group met the assumption of normality (W = 0.99, p > 0.05). The visual angle scores during the baseline block for the control group (W = 0.90, p < 0.001) and the PP group (W = 0.71, p < 0.001) did not meet the assumption of normality. The visual angle scores during the post-test block for the PP group met the assumption of normality (W =0.99, p > 0.05). The visual angle scores during the post-test block for the control group (W= 0.86, p < 0.001) and the MI group (W = 0.98, p < 0.05) did not meet the assumption of normality.

Histograms of the visual angle scores appeared normal (i.e., no noticeable skewness or kurtosis) (Figure 13). Square-root and log10 transformations were not feasible due to the visual angle scores having meaningful negative values. However, ANOVA is not sensitive to moderate deviations from normality; using non-normal distributions, simulation studies have shown that the false positive rate is not greatly affected by violating the normality assumption (Glass, 1972; Harwell et al., 1992; Lix et al., 1996). Further, a qqplot of the residuals (Figure 14) demonstrates that the residuals fall close to the diagonal line (inside the 95% confidence bands), indicating that the normality of residuals assumption was met. Thus, we proceeded with running the two-way ANOVA.



Figure 13. Normality plots. (A) Histograms demonstrating frequency of visual angle (°) scores across control, motor imagery, and physical practice groups during the baseline block. (B) Histograms demonstrating frequency of visual angle (°) scores across control, motor imagery, and physical practice groups during the post-test block.



Standard Normal Distribution Quantiles

Figure 14. QQ-plot. QQ-plot demonstrating standard normal distribution quantiles and the residuals from the ANOVA quantiles.

Levene's Test demonstrated that the assumption of homogeneity of variance was not met for the visual angle measures across the groups (PP, MI, and control), F(5,1314) =24.761, p > 0.05. However, the ANOVA is robust to heteroscedasticity if the sample sizes are equal (Box, 1953; David & Johnson, 1951; Glass et al., 1972; Horsnell, 1953). Thus, we proceeded with the two-way ANOVA.

5.3 Aftereffects

There was a large and significant main effect of group [F(2, 63) = 51.56, p < 0.001, $\eta^2 = 0.528$] and time point [F(1, 63) = 167.80, p < 0.001, $\eta^2 = 0.457$] (Figure 15). There was also a large and significant interaction effect of group and time point [$F(2,63) = 103.49, p < 0.001, \eta^2 = 0.510$]. Post-hoc analyses with a Tukey adjustment demonstrates that there was a significant difference in final test and baseline visual angle in the PP group, in that the final test visual angle ($M = 4.73^\circ$, $SD = 1.56^\circ$) was significantly greater than the baseline visual angle ($M = 0.026^\circ$, $SD = 0.63^\circ$). There were no significant differences between the final test and baseline visual angles in either the MI or control groups. Further, there was a significant difference between the PP group and MI group during the final test block, as the visual angle for the PP group ($M = 4.73^\circ$, $SD = 1.56^\circ$) was significantly greater than that of the MI group ($M = 0.34^\circ$, $SD = 0.96^\circ$). Visual angle for the PP group ($M = 4.73^\circ$, $SD = 1.56^\circ$) was also significantly different from that of the control group ($M = 0.34^\circ$, $SD = 1.04^\circ$) during the final test block. Lastly, no significant difference was found between the MI group and the control group during the final test block, p = 1.00.



Figure 15. Dot plot of main results. Mean visual angles scores (°) at baseline and final testing for control, motor imagery, and physical practice groups. Error bars represent standard deviation.

Chapter 6: Discussion

6.1 Overview of Findings

The primary objective of this study was to examine whether internal models were updated during motor imagery. Internal modelling involves both the forward model, which makes predictions about a movement outcome for smooth movement control, and the inverse model, which compares the desired state with the current state of the body to choose appropriate motor commands (Wolpert et al., 1995). The forward model and inverse model are critical for motor control during overt movement allowing for movement adaptation and improved motor skill performance; however, the involvement of internal models during motor imagery remains largely unknown. We explored internal modelling during motor imagery using prism adaptation and a reach and point task, where participants either (1) physically practiced (PP group) or (2) imagined (MI group) reaching and pointing to a target or (3) performed an unrelated imagined line drawing task (control group) during exposure to 17° leftward shifting prism lenses. If participants adapted to the new prism environment via updating internal models, then we would observe rightward horizontal pointing deviations (after effects). Thus, we hypothesized that if motor imagery updates internal models, then aftereffects would be present in the MI group, like that of the PP group and unlike that of the control group.

In line with prior research, and as per our hypothesis, the PP group demonstrated aftereffects, indicating updating of internal models during overt movement (McIntosh et al., 2019). No aftereffects were observed in the control group, suggesting that prism exposure alone was not enough to update internal models. Lastly, contrary to prior literature, no aftereffects were observed in the MI group, indicating that internal models were not

updated during motor imagery. These results provide evidence that motor imagery alone is not sufficient to adapt movements to new environments, and thus differs from overt movement.

6.2 A Comparison with Prior Literature

The finding here that internal models are not updated during motor imagery raises the question of what accounted for the difference in results from prior work. With due respect for prior work, it is likely that methodological issues contributed to the different outcomes, including low sample size, lack of a comparator group, and prism exposure.

We performed an a priori power analysis that indicated 22 participants per group was needed to measure a large effect between groups. The 22 participants in the present work are more than twice the number of participants per experimental group in the prior literature, and we observed a large effect. Michel et al. (2013), Rannaud Monany et al. (2022), and Fleury et al. (2023) did not perform a priori or post-hoc power analyses, did not report effect sizes, and had considerably smaller sample sizes ($n \le 10$ per group). Comparing results between studies proves challenging owing to these differences, as we cannot ensure the practical significance of the prior work. For instance, we cannot rule out the possibility that individual variance played a large role in observing aftereffects within the motor imagery groups in this prior literature.

In the present work, appropriate comparison groups were included by randomly assigning participants to (1) a PP group which was needed to demonstrate the expected effect – updating internal models with overt movement; (2) a MI group which was needed to demonstrate whether or not motor imagery practice can update internal models; and (3) a control group which was needed to demonstrate that prism exposure alone was not enough

to show true adaptation. In contrast, Rannaud Monany et al. (2022) did not include a physical practice comparison group, meaning that there was no experimental group to demonstrate the expected results of updating internal models during microgravity exposure (i.e., that arm swimming movement times would increase after exposure).

The prior work using prism exposure (Fleury et al., 2023; Michel et al., 2013) included less than half of the exposure trials recommended by the most recent metaanalysis for observing aftereffects of prism adaptation – i.e., 250 exposure trials over the durations of ~15 minutes (McIntosh et al., 2019). This low number of exposure trials decreases the certainty that the aftereffects observed in both studies reflected true adaptation. Conversely, the present work included the recommended number of exposure trials needed for true adaptation of the sensorimotor system to the new prism environment. Adhering to this recommendation provides confidence that the aftereffects observed in the PP group reflects true adaptation to the prism environment and, on the other hand, that the lack of adaptation in the MI group was not attributable to a methodological limitation.

Finally, our experiment observed that motor imagery practice does not update internal models, however it is difficult to tease apart recruiting and updating – we cannot make any conclusions on whether internal models were recruited; we can only conclude that internal models were not updated. This is because, unlike the experiment by Kilteni et al. (2018), we did not use an experimental protocol that isolated the process of recruiting internal models. Thus, we cannot conclude whether our experiment supported the results of Kilteni et al. (2018). More research looking at the recruitment of internal models in isolation of updating is needed to determine if internal models can be recruited (but not updated) during motor imagery practice. Ultimately, it is difficult to make comparisons between the current experiment and prior literature due to the limitations of the prior literature. However, we can be confident in our results due to adequately powering the study, including appropriate comparison groups, and using the recommended number of exposure trials to ensure true adaptation of the sensorimotor system. The finding that motor imagery cannot update internal models raises the question of how skill acquisition occurs via motor imagery. To answer this question, we look to Grush's motor emulation theory, physiological differences between motor imagery and overt movement, and theories of motor imagery that consider the perceptual-cognitive components of learning.

6.3 Motor Emulation Theory and Internal Models

Motor emulation theory posits that learning through motor imagery occurs because it is the conscious perception of a forward model's sensory predictions, but this process of learning does not involve updating internal models (Grush, 2004). Specifically, Grush suggests that adaptation in behaviour (or 'motor output') occurs through a **Kalman filter system** where, during an action, this system estimates the accuracy of sensory input and necessarily adjusts the amount of correction applied to improve the accuracy of the internal model; the amount of correction is known as the **Kalman gain**. In the motor emulation theory, motor imagery has a Kalman gain of zero, meaning that motor imagery *cannot* change the internal model's predictions. Accordingly, motor emulation theory provides an explanation for how we learn through motor imagery using internal models, an idea supported by Kilteni et al. (2018), while unequivocally stating that practice through motor imagery cannot update the predictions of the internal model, an idea supported by the findings of the current study. However, if this is true, then how can motor imagery

influence or change behaviour to allow for skill acquisition? Highlighting the differences between motor imagery and overt movement may help us identify ways in which we can leverage motor imagery for skill acquisition.

6.4 Differences between Motor Imagery and Physical Practice?

Given the dominance of motor simulation theory, which indicates motor imagery is a simulation of overt movement (Jeannerod, 2001; O'Shea & Moran, 2017), it is largely believed that learning skills through motor imagery was the same as overt movement. Despite this long-standing belief, this study and countless others have noted differences between motor imagery and overt movement, suggesting that motor imagery may influence behaviour *differently* than overt movement. For example, overt movement is consistently known to activate the neural regions associated with the modification and the execution of motor programs (i.e., cerebellar and cortical motor regions), whereas motor imagery more commonly activates regions associated with visuomotor transformation and generation of the motor program (i.e., frontal and parietal regions), with evidence suggesting that they are critically important to motor imagery performance (Hardwick et al., 2018; Hétu et al., 2013; Kraeutner et al., 2017; Kraeutner, Keeler, et al., 2016; McInnes et al., 2016; Oostra et al., 2016; Sirigu et al., 1996). In a longitudinal study in which participants trained on a dartthrowing task, motor imagery and overt movement were found to have different patterns of brain activity, and learning via motor imagery was found to be inferior to that occurring via overt movement (Kraeutner, Stratas, et al., 2020). For instance, compared to motor imagery, overt movement was shown to have greater activation of the cerebellum, a region critical for refining motor programs. The authors speculated that sensory feedback, available during overt movement, allowed for optimal error detection/correction to occur,

accounting for greater activation observed for the cerebellum during overt movement compared to motor imagery, and superior outcomes for overt movement. The need for sensory feedback to adapt behaviour and learn motor skills via overt movement supports our findings, as the MI group did not have access to sensory information at the terminus of the imagined reach and point movement and consequently did not demonstrate any aftereffects. While the need for sensory feedback explains the current findings, how motor imagery drives adaptation and learning when feedback is not available is still not clear. Perhaps being *aware* that errors have occurred is needed for motor imagery to effectively adapt to new environments, or perhaps motor imagery relies on something completely different, such as cognitive or perceptual representations of actions.

In regard to being aware of errors, or having *explicit knowledge* of errors, the PP group in the current study received terminal sensory feedback at the end of all reaching movements under prism exposure, allowing for the explicit knowledge that errors were made. Conversely, the MI group received no actual terminal sensory feedback during prism exposure and thus, to adapt to the prism environment, the MI group needed to *implicitly* learn to adapt to the prism environment. Prism adaptation results from an interplay of explicit and implicit learning where (1) during strategic control, early adaptation is driven by explicit knowledge of errors, allowing for rapid correction of movement errors and (2) during sensory realignment, true adaptation occurs through a slow process driven by implicit learning where internal models update and adapt to the new prism environment; aftereffects are the result of this slow implicit process of adaptation (Prablanc et al., 2020). Thus, motor imagery may rely on explicit knowledge of errors during the strategic control stage of prism adaptation to update internal models, and consequently generate aftereffects.

It is well established that motor imagery-based practice can result in improved performance outcomes and learning. Recent work by Ingram and colleagues demonstrated that over five days of training, participants training via motor imagery were able to learn a complex motor skill, and while the magnitude of learning was less than that of a group training via overt movement, it was significantly better than an overt movement group for which knowledge of results was withheld, and of a control group that merely attended to a stimulus (Ingram et al., 2019). Importantly, a follow-up study by the same authors explored how learning could occur in the absence of sensory feedback (Ingram et al., 2022). Here the authors showed that the motor imagery group self-reported errors resulting from task performance, and like that observed for overt movement, the magnitude of the errors was influenced by the speed and complexity of the movement to be learned, both known drivers of error during physically executed movements. Participant reports of explicit knowledge of errors in this work supports the notion that this is required for motor adaptation to occur via motor imagery. Indeed, researchers have recently theorized that feedback simulated during motor imagery ('predicted effects' or 'simulated effects') are used in internal models to alter motor programs and thus learning of the movement (Dahm & Rieger, 2019; Rieger et al., 2023; Solomon et al., 2022). Considered in the context of motor emulation theory, it may be that this simulated feedback serves to alter the gain of the Kalman filter, in turn resulting in tuning of the internal model necessary for learning to occur. Future research should investigate the role of explicit knowledge of errors during motor imagery-based practice and prism adaptation, as this explicit knowledge may be needed to change the predictions of the internal model and subsequently affect behaviour and drive skill acquisition.

Finally, it is important to consider the possibility that skill acquisition through motor imagery-based practice simply does not involve updating internal models. Perhaps learning through motor imagery is more *perceptual-cognitive* than *motor* in nature. While both motor simulation theory and motor emulation theory support that motor imagery uses the motor regions of the brain, there are several other theories suggesting that motor imagery-based learning is more perceptual-cognitive in nature, such as the motor-cognitive model, the perceptual-cognitive model, and the effects imagery model to name a few (for a full review see Hurst & Boe, 2022). Most recently, Frank and colleagues proposed the perceptual-cognitive scaffolding theory suggesting that practice through motor imagery links the perceptual and cognitive representations of actions and refines the higher order representation networks, resulting in motor learning (Frank et al., 2023). This theory posits that skill level will influence motor imagery-based practice effects as learning truly motor tasks should be more difficult when the individual has no prior physical practice experience. If this is the case, then this theory may explain why the MI group was unable to adapt to the prism environment, as the MI group would not have any perceptual or cognitive representations of the action in the prism environment to rehearse. Future research should compare individuals who have physical practice experience in a prism environment to individuals who do not, to examine whether motor imagery is more effective with prior physical experience.

Ultimately there are key differences between motor imagery and physical practice that may help to explain how motor imagery drives adaptation and learning. First, motor imagery is associated with less cerebellar activity, which may contribute to why motor imagery was unable to update internal models to the prism environment. Second, the MI group received no explicit information on errors, which may be needed for true adaptation

to the prism environment. And third, motor imagery-based learning may not involve internal models at all and rather it may be more perceptual in nature. Understanding these differences is critical to ensure appropriate use of motor imagery in rehabilitation of motor impairments that result from brain injuries.

6.5 Implications for the Use of Motor Imagery

Motor imagery is an effective tool for many applications including surgical education (Goble et al., 2021), improving functional performance post total knee arthroplasty (Li et al., 2022), and improving motor and task performance in healthy individuals (Dickstein & Deutsch, 2007). Although existing literature has demonstrated the presence of an effect for motor imagery use, little research has explored the magnitude of its effectiveness. A recent meta-analysis demonstrates that using motor imagery for stroke recovery is only moderately effective at best (Barclay et al., 2020). Given that recent literature, including the current study, suggests that motor imagery is not a simulation of overt movement, it is important to question whether motor imagery is being used as effectively as possible. Future research should synthesize the current knowledge on the differences between motor imagery and overt movement and generate new motor imagery theory highlighting these differences. By doing this we can determine if motor imagery can be used more effectively by focusing on the specific mechanisms through which learning occurs via motor imagery.

Overall, our results support that motor imagery is not a simulation of overt movement, contrary to the dominant motor simulation theory that is the current foundation for motor imagery use. Thus, more research is needed to understand how the mechanistic differences between motor imagery and overt movement may impact the use of motor

imagery. One possible avenue for research may be directing motor imagery practice to focus on motor skills that patients have *prior physical practice experience* in; this is informed by the current study suggesting that motor imagery cannot update internal models like that of overt movement and that this may be due to not having prior physical practice experience. Overall, the current study adds to our theoretical understanding of motor imagery-based learning and provides a backbone for clinicians who use motor imagery techniques as part of their practice.

6.6 Considerations

Participants in all groups were instructed to keep the prism lenses on during the prism exposure phase, but if participants experienced dizziness or nausea, they were allowed to remove the lenses during breaks between trials. Removal of prism lenses may promote de-adaptation, however we controlled for this risk by ensuring all groups received the same instructions, meaning that the removal of the prism lenses should not affect any one group more than the others. Additionally, participants were instructed to keep a fixed gaze on the screen to further minimize the risk of de-adaptation.

The experimental setup involved three random locations for the circular target (centre of the screen, 10% to the left of the centre, and 10% to the right of the center) that occurred during the exposure, baseline, and post-test blocks; these are the same target locations used in MacIntosh et al. (2019). One limitation of having the same target locations in the exposure, baseline, and post-test blocks is the potential for learning effects. Learning effects can mask the aftereffects as they would demonstrate that the participants learned the task, rather than truly adapting to the environment. However, given that we did not see any aftereffects in the control group, and that we ensured 250 exposure trials over

the duration of 15 minutes, we can be confident that the aftereffects that we observed reflects true adaptation. Future studies can consider removing the centre target from the familiarization and exposure blocks and only use the centre target during the baseline and post-test blocks; this may help eliminate the risk of learning effects.

Chapter 7: Conclusions

The current work demonstrates that motor imagery cannot update internal models to a prism environment, like that of overt movement. This adds to our understanding of motor imagery-based learning, as it suggests that motor imagery is not a simulation of overt movement. Our results align with the proposition of motor emulation theory that motor imagery cannot update internal models, but this does not answer the question of how motor imagery can change behaviour to allow for skill acquisition. Recognizing the differences between motor imagery and overt movement, including a pattern of brain activation that is unique to motor imagery, provides context for how motor imagery can drive skill acquisition. For instance, prism adaptation relies on both explicit knowledge of errors during strategic control and implicit learning during sensory realignment, thus it is possible that the lack of explicit knowledge of errors (via sensory feedback) precluded adaptation to the new environment via motor imagery. Future research should investigate if explicit knowledge of errors is needed prior to motor imagery to update internal models to new environments. Despite motor imagery's promise for acquiring skills, it's efficacy in practical application is mixed: for instance, a recent meta-analysis demonstrates that the efficacy of motor imagery in promoting functional recovery in stroke rehabilitation is moderate at best (Barclay et al., 2020). This finding may be attributed, at least in part, to the assumption that motor imagery is a simulation of physical practice, and thus motor imagery is applied using the same principles. The knowledge that motor imagery-based learning may depend on mechanisms different from that of overt movement should be leveraged to improve its effectiveness in practical applications such as rehabilitation.

References

- Adams, J. A. (1971). A closed-loop theory of motor learning. *Journal of Motor Behavior*, 3(2), 111–149. https://doi.org/10.1080/00222895.1971.10734898
- Agostini, F., Pezzi, L., Paoloni, M., Insabella, R., Attanasi, C., Bernetti, A., Saggini, R.,
 Mangone, M., & Paolucci, T. (2021). Motor imagery: A resource in the fatigue rehabilitation for return-to-work in multiple sclerosis patients—A mini systematic review. *Frontiers in Neurology*, *12*. https://doi.org/10.3389/fneur.2021.696276
- Baizer, J. S., Kralj-Hans, I., & Glickstein, M. (1999). Cerebellar lesions and prism adaptation in macaque monkeys. *Journal of Neurophysiology*, *81*(4), 1960–1965. https://doi.org/10.1152/jn.1999.81.4.1960
- Barclay, R. E., Stevenson, T. J., Poluha, W., Semenko, B., & Schubert, J. (2020). Mental practice for treating upper extremity deficits in individuals with hemiparesis after stroke. *Cochrane Database of Systematic Reviews*, 5(5), CD005950. https://doi.org/10.1002/14651858.CD005950.pub5
- Bastian, A. J. (2008). Understanding sensorimotor adaptation and learning for rehabilitation. *Current Opinion in Neurology*, 21(6), 628–633. https://doi.org/10.1097/WCO.0b013e328315a293
- Box, G. E. P. (1953). Non-normality and tests on variances. *Biometrika*, 40(3–4), 318–335. https://doi.org/10.1093/biomet/40.3-4.318
- Caligiore, D., Mustile, M., Spalletta, G., & Baldassarre, G. (2017). Action observation and motor imagery for rehabilitation in Parkinson's disease: A systematic review and an integrative hypothesis. *Neuroscience and Biobehavioral Reviews*, 72, 210–222. https://doi.org/10.1016/j.neubiorev.2016.11.005

- Chapman, H. L., Eramudugolla, R., Gavrilescu, M., Strudwick, M. W., Loftus, A., Cunnington, R., & Mattingley, J. B. (2010). Neural mechanisms underlying spatial realignment during adaptation to optical wedge prisms. *Neuropsychologia*, 48(9), 2595–2601. https://doi.org/10.1016/j.neuropsychologia.2010.05.006
- Coello, Y., Orliaguet, J. P., & Prablanc, C. (1996). Pointing movement in an artificial perturbing inertial field: A prospective paradigm for motor control study.
 Neuropsychologia, 34(9), 879–892. https://doi.org/10.1016/0028-3932(96)00003-6
- Dahm, S. F., & Rieger, M. (2016). Is there symmetry in motor imagery? Exploring different versions of the mental chronometry paradigm. *Attention, Perception & Psychophysics*, 78(6), 1794–1805. https://doi.org/10.3758/s13414-016-1112-9
- Dahm, S. F., & Rieger, M. (2019). Is imagery better than reality? Performance in imagined dart throwing. *Human Movement Science*, 66, 38–52. https://doi.org/10.1016/j.humov.2019.03.005
- David, F. N., & Johnson, N. L. (1951). The effect of non-normality on the power function of the F-test in the analysis of variance. *Biometrika*, 38(1–2), 43–57. https://doi.org/10.1093/biomet/38.1-2.43
- de Vries, S., & Mulder, T. (2007). Motor imagery and stroke rehabilitation: A critical discussion. *Journal of Rehabilitation Medicine*, 39(1), 5–13. https://doi.org/10.2340/16501977-0020
- Decety, J., Jeannerod, M., Durozard, D., & Baverel, G. (1993). Central activation of autonomic effectors during mental simulation of motor actions in man. *The Journal* of Physiology, 461, 549–563. https://doi.org/10.1113/jphysiol.1993.sp019528

- Decety, J., Jeannerod, M., Germain, M., & Pastene, J. (1991). Vegetative response during imagined movement is proportional to mental effort. *Behavioural Brain Research*, 42(1), 1–5. https://doi.org/10.1016/s0166-4328(05)80033-6
- Decety, J., Jeannerod, M., & Prablanc, C. (1989). The timing of mentally represented actions. *Behavioural Brain Research*, 34(1–2), 35–42. https://doi.org/10.1016/s0166-4328(89)80088-9
- Decety, J., & Michel, F. (1989). Comparative analysis of actual and mental movement times in two graphic tasks. *Brain and Cognition*, 11(1), 87–97. https://doi.org/10.1016/0278-2626(89)90007-9
- Dickstein, R., & Deutsch, J. E. (2007). Motor imagery in physical therapist practice. *Physical Therapy*, 87(7), 942–953. https://doi.org/10.2522/ptj.20060331
- Fitts, P. M., & Posner, M. I. (1967). *Human performance*. Brooks/Cole Human performance. https://psycnet.apa.org/fulltext/1967-35040-000.pdf
- Fleury, L. (2020). Revisiting sensorimotor adaptation: New insights from inter-task transfer of after-effects in prism adaptation [Université de Lyon]. https://theses.hal.science/tel-03525038/
- Fleury, L., Dreyer, L., El Makkaoui, R., Leroy, E., Rossetti, Y., & Collet, C. (2023). Intertask transfer of prism adaptation through motor imagery. *Brain Sciences*, 13(1). https://doi.org/10.3390/brainsci13010114

Fleury, L., Prablanc, C., & Priot, A.-E. (2019). Do prism and other adaptation paradigms really measure the same processes? *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*, *119*, 480–496. https://doi.org/10.1016/j.cortex.2019.07.012

- Frank, C., Kraeutner, S. N., Rieger, M., & Boe, S. G. (2023). Learning motor actions via imagery—Perceptual or motor learning? *Psychological Research*. https://doi.org/10.1007/s00426-022-01787-4
- Glass, G. V. (1972). Consequences of failure to meet assumptions underlying the fixed effects analyses of variance and covariance. https://play.google.com/store/books/details?id=f7BKtwAACAAJ
- Glass, G. V., Peckham, P. D., & Sanders, J. R. (1972). Consequences of failure to meet assumptions underlying the fixed effects analyses of variance and covariance. *Review of Educational Research*, 42(3), 237–288. https://doi.org/10.3102/00346543042003237
- Goble, M. S. L., Raison, N., Mekhaimar, A., Dasgupta, P., & Ahmed, K. (2021). Adapting motor imagery training protocols to surgical education: A systematic review and meta-analysis. *Surgical Innovation*, 28(3), 329–351. https://doi.org/10.1177/1553350621990480
- Grèzes, J., & Decety, J. (2001). Functional anatomy of execution, mental simulation, observation, and verb generation of actions: A meta-analysis. *Human Brain Mapping*, *12*(1), 1–19. https://doi.org/10.1002/1097-0193(200101)12:1<1::aidhbm10>3.0.co;2-v
- Grush, R. (2004). The emulation theory of representation: Motor control, imagery, and perception. *The Behavioral and Brain Sciences*, 27(3), 377–396. https://doi.org/10.1017/s0140525x04000093
- Guillot, A., & Collet, C. (2005). Duration of mentally simulated movement: A review. *Journal of Motor Behavior*, 37(1), 10–20. https://doi.org/10.3200/JMBR.37.1.10-20

- Hallett, M. (2007). Transcranial magnetic stimulation: A primer. *Neuron*, 55(2), 187–199. https://doi.org/10.1016/j.neuron.2007.06.026
- Hardwick, R. M., Caspers, S., Eickhoff, S. B., & Swinnen, S. P. (2018). Neural correlates of action: Comparing meta-analyses of imagery, observation, and execution. *Neuroscience and Biobehavioral Reviews*, 94, 31–44.
 https://doi.org/10.1016/j.neubiorev.2018.08.003
- Harwell, M. R., Rubinstein, E. N., Hayes, W. S., & Olds, C. C. (1992). Summarizing monte carlo results in methodological research: The one- and two-factor fixed effects ANOVA cases. *Journal of Educational and Behavioral Statistics*, *17*(4), 315–339. https://doi.org/10.3102/10769986017004315
- Herlihey, T. A., Black, S. E., & Ferber, S. (2012). Terminal, but not concurrent prism exposure produces perceptual aftereffects in healthy young adults. *Neuropsychologia*, 50(12), 2789–2795.
 https://doi.org/10.1016/j.neuropsychologia.2012.08.009
- Hétu, S., Grégoire, M., Saimpont, A., Coll, M.-P., Eugène, F., Michon, P.-E., & Jackson, P.
 L. (2013). The neural network of motor imagery: An ALE meta-analysis. *Neuroscience and Biobehavioral Reviews*, *37*(5), 930–949.
 https://doi.org/10.1016/j.neubiorev.2013.03.017
- Horak, F. B., & Diener, H. C. (1994). Cerebellar control of postural scaling and central set in stance. *Journal of Neurophysiology*, 72(2), 479–493. https://doi.org/10.1152/jn.1994.72.2.479
- Horsnell, G. (1953). The effect of unequal group variances on the F-Test for the homogeneity of group means. *Biometrika*, 40(1/2), 128–136. https://doi.org/10.2307/2333104
Hurst, A. J., & Boe, S. G. (2022). Imagining the way forward: A review of contemporary motor imagery theory. *Frontiers in Human Neuroscience*, 16, 1033493. https://doi.org/10.3389/fnhum.2022.1033493

Ingram, T. G. J., Hurst, A. J., Solomon, J. P., Stratas, A., & Boe, S. G. (2022). Imagined movement accuracy is strongly associated with drivers of overt movement error and weakly associated with imagery vividness. *Journal of Experimental Psychology. Human Perception and Performance*, *48*(12), 1362–1372. https://doi.org/10.1037/xhp0001064

- Ingram, T. G. J., Solomon, J. P., Westwood, D. A., & Boe, S. G. (2019). Movement related sensory feedback is not necessary for learning to execute a motor skill. *Behavioural Brain Research*, 359, 135–142. https://doi.org/10.1016/j.bbr.2018.10.030
- Ishikawa, T., Tomatsu, S., Izawa, J., & Kakei, S. (2016). The cerebro-cerebellum: Could it be loci of forward models? *Neuroscience Research*, 104, 72–79. https://doi.org/10.1016/j.neures.2015.12.003
- Jeannerod, M. (1995). Mental imagery in the motor context. *Neuropsychologia*, *33*(11), 1419–1432. https://doi.org/10.1016/0028-3932(95)00073-c
- Jeannerod, M. (2001). Neural simulation of action: A unifying mechanism for motor cognition. *NeuroImage*, *14*(1 Pt 2), S103-9. https://doi.org/10.1006/nimg.2001.0832
- Jenkinson, N., & Miall, R. C. (2010). Disruption of saccadic adaptation with repetitive transcranial magnetic stimulation of the posterior cerebellum in humans. *Cerebellum*, 9(4), 548–555. https://doi.org/10.1007/s12311-010-0193-6
- Keele, S. W. (1968). Movement control in skilled motor performance. *Psychological Bulletin*, 70(6p1), 387–403. https://doi.org/10.1037/h0026739

Kilteni, K., Andersson, B. J., Houborg, C., & Ehrsson, H. H. (2018). Motor imagery involves predicting the sensory consequences of the imagined movement. *Nature Communications*, 9(1), 1617. https://doi.org/10.1038/s41467-018-03989-0

Kraeutner, S. N., Eppler, S. N., Stratas, A., & Boe, S. G. (2020). Generate, maintain, manipulate? Exploring the multidimensional nature of motor imagery. *Psychology* of Sport and Exercise, 48, 101673.

https://doi.org/10.1016/j.psychsport.2020.101673

Kraeutner, S. N., Ingram, T. G. J., & Boe, S. G. (2017). The effector independent nature of motor imagery: Evidence from rTMS induced inhibition to the primary motor cortices. *Neuropsychologia*, 97, 1–8.

https://doi.org/10.1016/j.neuropsychologia.2017.01.023

- Kraeutner, S. N., Keeler, L. T., & Boe, S. G. (2016). Motor imagery-based skill acquisition disrupted following rTMS of the inferior parietal lobule. *Experimental Brain Research*, 234(2), 397–407. https://doi.org/10.1007/s00221-015-4472-9
- Kraeutner, S. N., MacKenzie, L. A., Westwood, D. A., & Boe, S. G. (2016). Characterizing skill acquisition through motor imagery with no prior physical practice. *Journal of Experimental Psychology. Human Perception and Performance*, 42(2), 257–265. https://doi.org/10.1037/xhp0000148

Kraeutner, S. N., Stratas, A., McArthur, J. L., Helmick, C. A., Westwood, D. A., & Boe, S.
G. (2020). Neural and behavioral outcomes differ following equivalent bouts of motor imagery or physical practice. *Journal of Cognitive Neuroscience*, *32*(8), 1590–1606. https://doi.org/10.1162/jocn_a_01575

Krakauer, J. W. (2006). Motor learning: Its relevance to stroke recovery and neurorehabilitation. *Current Opinion in Neurology*, 19(1), 84–90. https://doi.org/10.1097/01.wco.0000200544.29915.cc

Krakauer, J. W. (2009). Motor learning and consolidation: The case of visuomotor rotation. Advances in Experimental Medicine and Biology, 629, 405–421. https://doi.org/10.1007/978-0-387-77064-2_21

Krakauer, J. W., Hadjiosif, A. M., Xu, J., Wong, A. L., & Haith, A. M. (2019). Motor learning. *Comprehensive Physiology*, 9(2), 613–663. https://doi.org/10.1002/cphy.c170043

- Krakauer, J. W., Pine, Z. M., Ghilardi, M. F., & Ghez, C. (2000). Learning of visuomotor transformations for vectorial planning of reaching trajectories. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 20(23), 8916–8924. https://doi.org/10.1523/JNEUROSCI.20-23-08916.2000
- Küper, M., Wünnemann, M. J. S., Thürling, M., Stefanescu, R. M., Maderwald, S., Elles,
 H. G., Göricke, S., Ladd, M. E., & Timmann, D. (2014). Activation of the cerebellar cortex and the dentate nucleus in a prism adaptation fMRI study. *Human Brain Mapping*, *35*(4), 1574–1586. https://doi.org/10.1002/hbm.22274
- Lackner, J. R., & Dizio, P. (1994). Rapid adaptation to Coriolis force perturbations of arm trajectory. *Journal of Neurophysiology*, 72(1), 299–313. https://doi.org/10.1152/jn.1994.72.1.299
- Lewis, R. F., & Zee, D. S. (1993). Ocular motor disorders associated with cerebellar lesions: Pathophysiology and topical localization. *Revue Neurologique*, 149(11), 665–677. https://www.ncbi.nlm.nih.gov/pubmed/8091079

Li, R., Du, J., Yang, K., Wang, X., & Wang, W. (2022). Effectiveness of motor imagery for improving functional performance after total knee arthroplasty: A systematic review with meta-analysis. *Journal of Orthopaedic Surgery and Research*, 17(1), 65. https://doi.org/10.1186/s13018-022-02946-4

Lix, L. M., Keselman, J. C., & Keselman, H. J. (1996). Consequences of assumption violations revisited: A quantitative review of alternatives to the one-way analysis of variance "F" Test. *Review of Educational Research*, 66(4), 579–619. https://doi.org/10.2307/1170654

Luauté, J., Schwartz, S., Rossetti, Y., Spiridon, M., Rode, G., Boisson, D., & Vuilleumier,
P. (2009). Dynamic changes in brain activity during prism adaptation. *The Journal* of Neuroscience: The Official Journal of the Society for Neuroscience, 29(1), 169–178. https://doi.org/10.1523/JNEUROSCI.3054-08.2009

Malouin, F., Richards, C. L., Jackson, P. L., & Lafleur, M. F. (2007). The kinesthetic and visual imagery questionnaire (KVIQ) for assessing motor imagery in persons with physical disabilities: A reliability and construct validity study. *Journal of Neurologic Physical Therapy; LaCrosse*, *31*(1), 20–29.
https://ezproxy.library.dal.ca/login?url=https://www.proquest.com/trade-journals/kinesthetic-visual-imagery-questionnaire-kviq/docview/213736127/se-2

Martin, T. A., Keating, J. G., Goodkin, H. P., Bastian, A. J., & Thach, W. T. (1996).
Throwing while looking through prisms. I. Focal olivocerebellar lesions impair adaptation. *Brain: A Journal of Neurology*, *119 (Pt 4)*, 1183–1198.
https://doi.org/10.1093/brain/119.4.1183

- Maschke, M., Gomez, C. M., Ebner, T. J., & Konczak, J. (2004). Hereditary cerebellar ataxia progressively impairs force adaptation during goal-directed arm movements. *Journal of Neurophysiology*, 91(1), 230–238. https://doi.org/10.1152/jn.00557.2003
- McInnes, K., Friesen, C., & Boe, S. (2016). Specific brain lesions impair explicit motor imagery ability: A systematic review of the evidence. *Archives of Physical Medicine* and Rehabilitation, 97(3), 478-489.e1. https://doi.org/10.1016/j.apmr.2015.07.012
- McIntosh, R. D., Brown, B. M. A., & Young, L. (2019). Meta-analysis of the visuospatial aftereffects of prism adaptation, with two novel experiments. *Cortex*, *111*, 256–273. https://doi.org/10.1016/j.cortex.2018.11.013
- Miall, R. C., Christensen, L. O. D., Cain, O., & Stanley, J. (2007). Disruption of state estimation in the human lateral cerebellum. *PLoS Biology*, 5(11), e316. https://doi.org/10.1371/journal.pbio.0050316
- Miall, R. C., & Wolpert, D. M. (1996). Forward models for physiological motor control.
 Neural Networks: The Official Journal of the International Neural Network Society, 9(8), 1265–1279. https://doi.org/10.1016/S0893-6080(96)00035-4
- Michel, C., Gaveau, J., Pozzo, T., & Papaxanthis, C. (2013). Prism adaptation by mental practice. *Cortex*, 49(8), 2249–2259. https://doi.org/10.1016/j.cortex.2012.11.008
- Morton, S. M., & Bastian, A. J. (2006). Cerebellar contributions to locomotor adaptations during splitbelt treadmill walking. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *26*(36), 9107–9116.
 https://doi.org/10.1523/JNEUROSCI.2622-06.2006
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*(1), 97–113. https://doi.org/10.1016/0028-3932(71)90067-4

- Oostra, K. M., Van Bladel, A., Vanhoonacker, A. C. L., & Vingerhoets, G. (2016). Damage to fronto-parietal networks impairs motor imagery ability after stroke: A voxelbased lesion symptom mapping study. *Frontiers in Behavioral Neuroscience*, 10, 5. https://doi.org/10.3389/fnbeh.2016.00005
- O'Shea, H., & Moran, A. (2017). Does motor simulation theory explain the cognitive mechanisms underlying motor imagery? A critical review. *Frontiers in Human Neuroscience*, *11*, 72. https://doi.org/10.3389/fnhum.2017.00072
- Panico, F., Rossetti, Y., & Trojano, L. (2020). On the mechanisms underlying prism adaptation: A review of neuro-imaging and neuro-stimulation studies. *Cortex*, 123, 57–71. https://doi.org/10.1016/j.cortex.2019.10.003
- Panico, F., Sagliano, L., Grossi, D., & Trojano, L. (2016). Cerebellar cathodal tDCS interferes with recalibration and spatial realignment during prism adaptation procedure in healthy subjects. *Brain and Cognition*, 105, 1–8. https://doi.org/10.1016/j.bandc.2016.03.002
- Panouillères, M., Neggers, S. F. W., Gutteling, T. P., Salemme, R., van der Stigchel, S., van der Geest, J. N., Frens, M. A., & Pélisson, D. (2012). Transcranial magnetic stimulation and motor plasticity in human lateral cerebellum: dual effect on saccadic adaptation. *Human Brain Mapping*, *33*(7), 1512–1525. https://doi.org/10.1002/hbm.21301
- Papaxanthis, C., Pozzo, T., Skoura, X., & Schieppati, M. (2002). Does order and timing in performance of imagined and actual movements affect the motor imagery process?
 The duration of walking and writing task. *Behavioural Brain Research*, *134*(1–2), 209–215. https://doi.org/10.1016/s0166-4328(02)00030-x

Papaxanthis, C., Schieppati, M., Gentili, R., & Pozzo, T. (2002). Imagined and actual arm movements have similar durations when performed under different conditions of direction and mass. *Experimental Brain Research. Experimentelle Hirnforschung. Experimentation Cerebrale*, *143*(4), 447–452. https://doi.org/10.1007/s00221-002-1012-1

Prablanc, C., Panico, F., Fleury, L., Pisella, L., Nijboer, T., Kitazawa, S., & Rossetti, Y. (2020). Adapting terminology: Clarifying prism adaptation vocabulary, concepts, and methods. *Neuroscience Research*, 153, 8–21. https://doi.org/10.1016/j.neures.2019.03.003

- Prablanc, C., Tzavaras, A., & Jeannerod, M. (1975). Adaptation of hand tracking to rotated visual coordinates. *Perception & Psychophysics*, 17(3), 325–328. https://doi.org/10.3758/BF03203218
- Rannaud Monany, D., Barbiero, M., Lebon, F., Babič, J., Blohm, G., Nozaki, D., & White, O. (2022). Motor imagery helps updating internal models during microgravity exposure. *Journal of Neurophysiology*, *127*(2), 434–443. https://doi.org/10.1152/jn.00214.2021
- Redding, G. M., Rossetti, Y., & Wallace, B. (2005). Applications of prism adaptation: a tutorial in theory and method. *Neuroscience and Biobehavioral Reviews*, 29(3), 431–444. https://doi.org/10.1016/j.neubiorev.2004.12.004
- Redding, G. M., & Wallace, B. (1988). Components of prism adaptation in terminal and concurrent exposure: organization of the eye-hand coordination loop. *Perception & Psychophysics*, 44(1), 59–68. https://doi.org/10.3758/bf03207476

- Redding, G. M., & Wallace, B. (1993). Adaptive coordination and alignment of eye and hand. *Journal of Motor Behavior*, 25(2), 75–88. https://doi.org/10.1080/00222895.1993.9941642
- Rieger, M., Boe, S. G., Ingram, T. G. J., Bart, V. K. E., & Dahm, S. F. (2023). A theoretical perspective on action consequences in action imagery: Internal prediction as an essential mechanism to detect errors. *Psychological Research*. https://doi.org/10.1007/s00426-023-01812-0
- Schmidt, R. A. (1975). A schema theory of discrete motor skill learning. *Psychological Review*, 82(4), 225–260. https://doi.org/10.1037/h0076770
- Shadmehr, R., & Mussa-Ivaldi, F. A. (1994). Adaptive representation of dynamics during learning of a motor task. *The Journal of Neuroscience*, 14(5), 3208–3224. https://doi.org/10.1523/JNEUROSCI.14-05-03208.1994
- Sirigu, A., Duhamel, J. R., Cohen, L., Pillon, B., Dubois, B., & Agid, Y. (1996). The mental representation of hand movements after parietal cortex damage. *Science*, 273(5281), 1564–1568. https://doi.org/10.1126/science.273.5281.1564
- Solomon, J. P., Hurst, A. J., Lee, J., & Boe, S. G. (2022). Are observed effects of movement simulated during motor imagery performance? *Behavioral Neuroscience*, *136*(3), 264–275. https://doi.org/10.1037/bne0000517
- Solomon, J. P., Kraeutner, S. N., O'Neil, K., & Boe, S. G. (2021). Examining the role of the supplementary motor area in motor imagery-based skill acquisition. *Experimental Brain Research. Experimentelle Hirnforschung. Experimentation Cerebrale*, 239(12), 3649–3659. https://doi.org/10.1007/s00221-021-06232-3

- Stevens, J. A., & Stoykov, M. E. P. (2003). Using motor imagery in the rehabilitation of hemiparesis. Archives of Physical Medicine and Rehabilitation, 84(7), 1090–1092. https://doi.org/10.1016/s0003-9993(03)00042-x
- Tseng, Y.-W., Diedrichsen, J., Krakauer, J. W., Shadmehr, R., & Bastian, A. J. (2007). Sensory prediction errors drive cerebellum-dependent adaptation of reaching. *Journal of Neurophysiology*, 98(1), 54–62. https://doi.org/10.1152/jn.00266.2007
- Weiner, M. J., Hallett, M., & Funkenstein, H. H. (1983). Adaptation to lateral displacement of vision in patients with lesions of the central nervous system. *Neurology*, 33(6), 766–772. https://doi.org/10.1212/wnl.33.6.766
- Wolpert, D. M., Ghahramani, Z., & Jordan, M. I. (1995). An internal model for sensorimotor integration. *Science*, 269(5232), 1880–1882. https://doi.org/10.1126/science.7569931
- Wolpert, D. M., Miall, R. C., & Kawato, M. (1998). Internal models in the cerebellum. *Trends in Cognitive Sciences*, 2(9), 338–347. https://doi.org/10.1016/s1364-6613(98)01221-2
- Zimmermann-Schlatter, A., Schuster, C., Puhan, M. A., Siekierka, E., & Steurer, J. (2008).
 Efficacy of motor imagery in post-stroke rehabilitation: A systematic review. *Journal of Neuroengineering and Rehabilitation*, 5, 8. https://doi.org/10.1186/1743-0003-5-8

Appendix A: Recruitment Materials – Posters

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

Volunteers Needed...

What: We are recruiting for a study examining the mechanisms of learning during motor imagery practice.

The study involves wearing special prism lenses and reaching towards a target on a touchscreen monitor. You will visit the Laboratory for Brain Recovery and Function at



Dalhousie University for a single session lasting 60 minutes. You will be compensated \$15.

Eligibility: Volunteers must be 17+ years of age and have no history of disorders affecting the brain, nerves, bones, or muscles that would impact your ability to complete the study.

Where: Rm 426 Forrest Building, Dalhousie University

Principal Investigator: Dr. Shaun Boe

Contact: Juliet Rowe

If interested or have any questions, please email or apply via the QR code:

juliet.rowe@dal.ca or



Appendix B: Assessments

Edinburgh Handedness Inventory

Please indicate your preferences in the use of hands in the following activities by putting a check in the appropriate column. Where the preference is so strong that you would never try to use the other hand, unless absolutely forced to, put 2 checks. If in any case you are really indifferent, put a check in both columns.

Some of the activities listed below require the use of both hands. In these cases, the part of the task, or object, for which hand preference is wanted is indicated in parentheses.

Please try and answer all of the questions, and only leave a blank if you have no experience at all with the object or task.

	Left	Right		
1. Writing				
2. Drawing				
3. Throwing				
4. Scissors				
5. Toothbrush				
6. Knife (without fork)				
7. Spoon				
8. Broom (upper hand)				
9. Striking Match (match)				
10. Opening box (lid)				
<u>TOTAL(count checks in</u> both columns)				

Difference	Cumulative TOTAL	Result

Scoring:

Add up the number of checks in the "Left" and "Right" columns and enter in the "TOTAL" row for each column. Add the left total and the right total and enter in the "Cumulative TOTAL" cell. Subtract the left total from the right total and enter in the "Difference" cell. Divide the "Difference" cell by the "Cumulative TOTAL" cell (round to 2 digits if necessary) and multiply by 100; enter the result in the "Result" cell.

Interpretation (based on Result): below -40 = left-handed between -40 and +40 = ambidextrous above +40 = right-handed

Kinesthetic and Visual Imagery Questionnaire (KVIQ)

Quantifying Imagined Movement in Non-Disabled and Pathological Systems

Participant Information								
Participant Code:	Group:	Sex:	Age:	Date (dd/mm/yy): / /				
			_	-				
SCORING: KVIQ								
Movement		Visual	Kinesthetic	Comments				
Forward shoulder flexi	on	/ 5	/ 5					
Thumb-fingers opposit	tion	/ 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
Tot	als		/25 /25								

KVIQ Script:

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

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

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

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

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

Do you have any questions?

-- No

Let's begin. Here is the first movement.

- o Demonstrate the "forward shoulder flexion" of the Non-Dominant hand
- o 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 1^{rd} 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

CLARITY – THIRD PERSON PERSPECTIVE

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

INTENSITY – FIRST PERSON PERSPECTIVE

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



Project title: Adapting to Prisms during Motor Imagery Practice

Lead researcher:

Dr. Shaun Boe Professor, School of Physiotherapy Dalhousie University Email: s.boe@dal.ca

Other researchers

Juliet Rowe MSc Candidate, School of Physiotherapy Dalhousie University Email: juliet.rowe@dal.ca

Funding provided by: The Natural Sciences & Engineering Research Council (NSERC)

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 to think about it. Mark anything you do not understand or want explained better. After you 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

Purpose and Outline of the Research Study

Motor imagery is when someone imagines themselves doing a movement in their head, without actually moving. Motor imagery can be used to learn and improve movements and is used in settings like sports and physical therapy.

Although motor imagery practice has been shown to be effective for improving performance in sports and helping people recover after injuries, we still understand very little about how it works. For example, we are unsure about the processes of how motor imagery helps people learn or improve movement. Some researchers have found evidence that the processes of motor imagery are like when we physically perform movement. When we physically perform a movement however, we can adapt to changing environmental conditions to allow for accurate and precise movement. When we do motor imagery there is no feedback from performing the movement. When we do motor imagery there is no feedback as we don't actually perform the movement. The purpose of this study is to determine whether individuals can adapt to new environmental conditions during motor imagery practice even in the absence of feedback about the movement.

The information gathered in this study will contribute to our understanding of how we learn through motor imagery and will help us to design better training programs for sports and rehabilitation. More information about the study will be provided to you when your participation is complete.

Who Can Take Part in the Research Study

You may participate in this study if you are at least 17 years of age, have normal or corrected-to-normal vision (that is you wear glasses or contact lenses), and if you have no neuromuscular (brain or nerve) or musculoskeletal (muscle or bone) disorders that in your judgement would impede your ability to complete the study.

What You Will Be Asked to Do

In this study, we will ask you to complete a few assessments and a simple reach and point task on a touchscreen monitor. The study will take approximately 60 minutes to complete. The assessments and reach and point task procedure are described below:

A Questionnaire that Measures Handedness

This questionnaire will measure how right- or left-handed you are. We will ask you to complete this questionnaire at the beginning of the study session. To complete this questionnaire, you will be given a list of 10 everyday, common, one-handed tasks. You will be asked which hand you use to perform these tasks. This information will allow us to determine whether you are right- or left-handed.

A Questionnaire that Measures Motor Imagery Ability

This questionnaire will measure how vividly you are imagining a movement. We will ask you to complete this questionnaire at the beginning of the study session. To complete this questionnaire, we will show you how to do a movement, ask you to perform the movement, and then ask you to imagine yourself performing the movement. We will then ask you to rate how well you imagine performing the movement compared to actually performing it. This information will allow us to determine how well you can perform 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 shoulder. Because of the location of these electrodes, it would be best to wear a sleeveless or short-sleeved shirt for the study. We can provide a t-shirt (size S, M, and L) and a change room if needed.

Reach and Point Task

We will ask you to perform a simple reach and point task. During the task, a target (a small circle) will appear on a touchscreen monitor at random locations, and your task will be to reach forward and touch the target as quickly and accurately as possible. Once you have touched the target, you will return your hand back to its starting position. For the duration of the reach and point task, we will be recording muscle activity from the shoulder you are using to perform the task.

On some trials, instead of physically pointing to the target, you may be asked instead to vividly imagine what it would look like and feel like to reach forward and touch the target. On other trials, you may be asked to imagine the distance between your starting hand position and the target, without performing or imagining the reach and point movement.

Possible Benefits, Risks and Discomforts

Participating in the study might not benefit you, but through this research we may learn things that will benefit others. This study has the potential to benefit society through the generation of knowledge regarding learning through imagined movement and the potential to inform the application of different training methods for athletes and people who experience challenges with movement resulting from brain injuries, like stroke.

The risks associated with this study are minimal; though you may become bored or fatigued during the session, you will be offered breaks between activities to reduce these risks. There is minimal risk related to the use of electromyography (i.e., the

technique we use to record muscle activity). The electrodes lie on top of the skin (like a sticker) and a conductive gel provides 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 thanked for your participation with your choice of 1 SONA point (if you have not reached the allowable maximum) or \$15. You will be compensated regardless of whether you complete the session; if you choose to withdraw from the study at any point, it will have no effect on your compensation.

How your information will be protected

<u>Privacy</u>: 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, age, or student ID) 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. Other than your name and signature on the consent form, the only personal details collected in this study are your age, sex, and handedness for the purpose of summarizing the study demographics.

<u>Confidentiality</u>: In order to protect your privacy and keep your participation in the study confidential, your data will be anonymized. For the purpose of data analyses, all participants will only be identified by their study code (i.e., P001). All hard copy data associated with the study (including this consent form) will be stored 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.

<u>Data retention</u>: Information that you provide 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 **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 in a secure, password protected server in the Laboratory for Brain Recovery and

Function. In the event that a publisher requires study data to be a part of a public data repository (where data is stored and can be accessed by members of the public to improve transparency in science) only anonymized data is included, meaning that you will not be identified in any way.

If You Decide to Stop Participating

You may choose to stop participating in the study at any time (i.e., during questionnaire completion or during the reach and point task) and will still be compensated as if you had completed the full session. If you choose to withdraw from the study during the session, your data will be deleted immediately when the experiment program exits. You can also contact the research team at any time within 6 months of your participation and ask that your data be removed from the study. After the 6-month period your data will be entered into the final analysis and can no longer be removed.

How to Obtain Results

If you would like to see the results of the study, you can obtain a short description of the findings by visiting the Laboratory for Brain Recovery and Function website (<u>boelab.com</u>) in approximately 12 months. No individual results will be provided. Additionally, you can contact the research team using the information on this form and request that a copy of the final manuscript is sent to you once it has been published.

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 contact the principal investigator, Dr. Shaun Boe (phone: (902) 494-6360, email: <u>s.boe@dal.ca</u>), or Juliet Rowe (email: <u>juliet.rowe@dal.ca</u>) at any time with questions, comments or, concerns about the research study.

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 # 2023-6649).

Other

None of the members of the research team have any financial interest in the outcome of this study.

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: Adapting to Prisms during Motor Imagery PracticeLead researcher:

Dr. Shaun Boe Professor, School of Physiotherapy Dalhousie University Email: s.boe@dal.ca

Other researchers

Juliet Rowe MSc Candidate, School of Physiotherapy Dalhousie University Email: juliet.rowe@dal.ca

I have read the explanation about this study. I have been given the opportunity to discuss it and my questions have been answered to my satisfaction.

I understand that I have been asked to take part in a single session and I agree to take part in this study. I agree that my study information may be used as described in this consent form.

My participation is voluntary, and I understand that I am free to withdraw from the study at any time throughout the session.

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

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

Appendix D: Debriefing Materials

Debriefing Letter

Project title: Adapting to Prism during Motor Imagery Practice

REB file number: 2023-6649

Thank you for taking the time to participate in our study! Your data will help us better understand how we learn through motor imagery.

At the onset of this study, you were provided with a vague (but accurate) description of the study's purpose and the methods of the experiment. Now that you have completed the session, we can explain the design of the study in greater detail without the risk of influencing your performance on the task.

As stated in the consent form, the purpose of this study is to determine whether individuals can adapt to new environmental conditions during motor imagery practice. To test this, we randomly assigned participants to groups that practiced a reach and point task either physically, with motor imagery (imagine what it would look like and feel like to reach and point to the target) or performed an un-related task (imagine drawing a line between the target and your finger). All groups completed an identical familiarization and baseline blocks of the reach and point task but performed different tasks in the prism condition block: groups either practice only physical practice trials, motor imagery trials, control trials, or they practiced a combination of the trial types (i.e., physical practice and motor imagery or physical practice and control). The last testing block of the reach and point task was the same for all three groups.

If motor imagery can adapt to new environmental conditions (i.e., the prism condition), then participants in the motor imagery groups should have similar performance to the physical practice group in the final testing block. Specifically, we are looking for presence of aftereffects, which would involve pointing rightwards of the target in the final testing block.

Once the study is complete, a summary of our findings will be posted on our lab's website (boelab.ca) for you to view. Additionally, you can email the research team and ask to be notified when the study is published! Thank you again for your time!