Mechanisms Underlying the Learning of Skilled Movement Execution via Motor Imagery

by

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Dalhousie University is located in Mi'kma'ki, the
ancestral and unceded territory of the Mi'kmaq.
We are all treaty people.

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LIST OF ABBREVIATIONS USED

BVE — Bivariate Variable Error
CI — Credible Interval
CT — Control Task
DLPFC — Dorsolateral Prefrontal Cortex
EEG — Electroencephalography
EMG — Electromyography
EOG — Electrooculography
ES — Effect Size
HPDI — Highest Posterior Density Interval
IPL — Inferior Parietal Lobule
MI — Motor Imagery
MIT — Motor Imagery Training
MT — Movement Time
OM — Overt Movement
PC — Perceptual Control
PMA — Premotor Area
PMBS — Post-Movement Beta Synchronization
PP — Physical Practice
PPC — Posterior Parietal Cortex
PPFB — Physical Practice with Additional Feedback
PT — Physical Training
RE — Radial Error
SAF — Speed Accuracy Function
SD — Standard Deviation
SMA — Supplementary Motor Area
SPL — Superior Parietal Lobule
SRT — Serial Reaction Time

ABSTRACT

Learning to move skillfully is a fundamental behaviour. Motor skills can be learned even in the absence of overt bodily movement through a process known as motor imagery — the mental rehearsal of movement — which has promising applications in rehabilitation. However, the mechanisms underlying imagery-based motor learning are not well understood and learning may be attributed to improvements in perceptual or cognitive processes rather than improvement in movement execution itself. The research projects presented in this dissertation aimed to investigate whether motor imagery is capable of driving improvements in movement execution and if so, what the underlying mechanisms of this might be and how they differ from that of overt practice. Using a novel experimental task designed to answer this question, the findings presented here suggest that motor imagery is indeed capable of driving the learning of skilled movement execution, though of a lesser magnitude than overt practice. In the absence of sensory feedback, motor imagery appears capable of determining the accuracy of an imagined movement. Neuroimaging results demonstrated that imagined movement accuracy was associated with similar brain regions as overt movement accuracy but with substantially different activation patterns. Together these results suggest that motor imagery appears to afford one with a prediction of the motor and sensory consequences of an imagined movement such that a comparison can be made with intended consequences, which provides a basis for improving subsequent movement attempts, imagined or otherwise. These results highlight the importance of minding experimental design when studying motor imagery and validating its utility for clinical applications.

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CHAPTER 1 | INTRODUCTION

1.0. GENERAL INTRODUCTION

"… to move things is all mankind can do… whether in whispering a syllable, or in felling a forest." — Sir Charles Scott Sherrington

Movement is our only means of affecting the outside world [1]. While our brains sense the environment through numerous inputs — our senses of sight, touch, smell, taste, and hearing — our only output is movement. This includes everything from our ability to walk from one point to another, to our ability to speak. It is therefore no surprise that scientists are deeply interested in the neuroscience of movement. One of the more fascinating features of human movement is our ability to learn and adapt to the changing demands of our environment. This process of improving our movement abilities is referred to as motor learning in the academic literature [2–4]. Motor learning has been studied using a variety of techniques and theoretical perspectives, including animal studies of cellular mechanisms [5,6], computational modelling [4], and behavioural experiments involving humans that are often coupled with neuroimaging technologies [7]. Interestingly, motor learning may not require movement itself. Decades of research has affirmed the notion that one can learn skilled movement not just by physically practicing, but by observing others [8], or even simply imagining oneself performing the skill [9]. How motor learning can occur during imagery is poorly understood compared to our understanding of how it occurs with overt movement. This dissertation will explore how this is possible, and what it means for our understanding of human movement and the mind.

Academics typically refer to the mental performance of movement as motor imagery [10–12]. The deliberate use of motor imagery to drive motor learning is often referred to as "mental practice", particularly in the sport or musical training contexts. Motor imagery has been demonstrated to be an effective means of driving motor learning in many contexts, such as sports, music, and vocational training, and shows promise for rehabilitation [13–16]. Motor imagery has also received considerable academic attention for its potential role in brain computer interfaces that allow the control of computers or robots without relying on movement for input [17–19]. Neuroimaging studies have revealed striking similarities between motor imagery and motor execution with respect to which brain regions and networks are involved [20–24]. These findings suggest that motor imagery may drive motor learning via similar mechanisms as that of overt practice. However, explaining skill acquisition via motor imagery by citing its similarity with motor execution leaves much to be desired. First and foremost, these are fundamentally different behaviours: one involves overtly moving the body, and the other does not. Second, neuroimaging studies do not support a perfect overlap in brain regions associated with motor imagery and execution — there are differences anatomically and functionally [20,23]. And finally, while sensory feedback plays a central role in motor learning via overt practice [25], feedback is not present in the absence of movement. How exactly motor learning is possible via motor imagery is a difficult question to answer. As with many fields of research, neuroscience seeks to understand a "black box". Typically, neuroscience is able to proceed by manipulating the inputs to the brain and observing what happens to the outputs. But motor imagery is short on outputs.

This dissertation aims to investigate how motor imagery can drive motor learning in the absence of sensory feedback. Key to this series of research projects is first testing the assumption that motor imagery does drive motor learning. That is, that performance improvements in movement quality over time are not due to other mechanisms like perceptual learning [26]. To test this assumption, motor learning via imagery was compared to overt practice using a new experimental task where participants learned to better execute a specific, novel movement pattern while controlling for general task improvements and perceptual or observational learning. Next, this work was built upon by attempting to investigate whether motor learning in fact does allow for error-based learning, perhaps by assessing the accuracy of a simulation [27]. Finally, we employed the same experimental task but with the addition of neuroimaging using electroencephalography (EEG) and modern statistical techniques to identify brain activity patterns that may indicate error detection during motor imagery. Theoretically, learning how motor imagery might drive learning without sensory feedback is an inherently interesting question that may contribute to neuroscience generally. Pragmatically, a better understanding of how motor imagery works may provide insight about how to best harness its positive effects outside the laboratory.

1.1. MOTOR CONTROL & LEARNING

Our remarkable ability to learn is central to our success as a species. It's why we can get home, know what we can or cannot eat, speak to one another, pursue science, and build technology. What knowledge and skills are innate and what is learned give rise to debates about "nature versus nurture", and even figure into discussions about how we should judge one another's actions and determine fundamental human rights. It is not surprising that large portions of the fields of psychology and neuroscience are dedicated to understanding learning and memory. Learning refers to the process of acquiring knowledge, and memory refers to the retention and reconstruction of that knowledge [28]. Over the decades, this highly active field of research has classified learning and memory into numerous types depending on such characteristics as time scale (e.g., short- or long-term memory), the type of knowledge (e.g., declarative versus procedural), mechanism of learning (e.g., associative versus non-associative), and more [29]. Learning can also be categorized by domain: cognitive, affective, and psychomotor [30]. Motor learning is widely studied in psychology and neuroscience given its amenability to sophisticated research techniques. Compared to behaviours like understanding language or social behaviour, motor output is relatively straightforward to measure objectively. Further, motor learning can be modelled more readily in animal models [6] — it's hard to have a conversation with a mouse about how it feels, but you can watch it move — which means more cutting-edge research techniques can be applied and at a large scale. Motor learning is thus researched at various measurement scales and levels of complexity, providing a useful framework upon which psychology and neuroscience may be able to derive generalizable principles of learning.

Fitts and Posner famously proposed that the learning of motor skills consisted of three temporal phases: cognitive, associative, and autonomous [31]. The cognitive stage is characterized by identifying potential solutions to a movement problem. An important aspect of this stage is that it requires explicit knowledge of the movement being learned. Once a potential solution is identified and practice ensues, the learner enters the associative stage. This involves exploring the solution and making refinements based on task success — that is, actions are associated with successful outcomes. Finally, once sufficient practice has occurred the learner enters the autonomous stage where performance becomes a matter of executing a well refined skill that requires little cognitive effort. While it is true that evidence has generally supported the existence of these stages of motor learning [32], it now seems clear that they are not easily parsed, and much overlap exists [33]. Further, some believe that while a highly skilled action may be performed in an "automatic" nature, the useful application of this skill requires knowledge of context to determine when to execute a given action or some variation of it — which still requires conscious awareness [34] — and deliberative decisions can affect motor reflexes [35], demonstrating that the distinction between cognitive and motor skills is an oversimplification. While understanding learning in terms of its temporal stages is a useful construct given that learning refers to a change over time, a deeper understanding is needed.

Developing a thorough understanding of how motor learning occurs requires analysis at many levels. Marr's levels of analysis provide a useful framework in this regard [36,37]. At the computational or behavioural level of analysis, one attempts to understand what a system does and why (i.e., what problem is the system trying to solve). At the algorithmic or representational level, one is concerned with how a system solves problems; that is, how information is represented and manipulated by the system to achieve its goals. Finally, at the implementational level one works to understand what exists to physically implement the algorithms used to solve problems. As an example, most people are aware of what their computer can do for them (computational/behavioural level), but likely know far less about how the software code and algorithms work (algorithmic/representational level), or how the hardware implements that software (implementational level). In the case of motor learning, the implementational level refers to what neural structures and functions are responsible for learning to solve movement problems. Research at each level of analysis can inform and complement one another. It is possible that realities at the neural level constrain what processing is reasonable at the algorithmic level, and therefore what computations can be performed. As an example, from the motor control literature, neural processing of sensory feedback is too slow to have any meaningful corrective effect on a sufficiently fast movement, which is partly what motivates the existence of so-called forward models, which will be discussed below [38]. As a comprehensive understanding of motor learning appears best achieved by familiarizing oneself with each level of analysis, this chapter will review the literature broadly using this framework. It should be noted that it is not reasonable to discuss each level in complete isolation, and overlap should be expected and will in fact be highlighted where possible to facilitate completeness. Throughout the chapter, motor control literature will be reviewed as needed to provide context for understanding motor learning.

1.2. WHAT DOES THE MOTOR SYSTEM DO? BEHAVIOURAL / COMPUTATIONAL LEVEL OF ANALYSIS

A large portion of the field of motor control and learning is dedicated to characterizing the motor system solely at the behavioural level [39]. Much work at this level of analysis involves developing computational models of behaviour and testing their predictions. One of the earliest examples of this line of work includes Fitts's Law [40]. Fitts proposed a metric of difficulty for a target selection task — that is, the act of pointing.

The law predicts that the time required to move to a target area is a function of the ratio between the distance to the target and the width of the target. For instance, a longer distance requires more time, and a wider target requires less time given that precision becomes less important. Constraining certain parameters, such as distance to and width of the target, can allow for a measure of skill based on the time a participant achieves. Fitts's law was allegedly a major factor in Xerox's decision to commercialize the computer mouse. Another example of early computational work includes the Bernstein degrees of freedom problem [41], which describes the redundancy that exists in the motor system for solving a given problem. For instance, pointing to a target can be accomplished in many equally effective ways (paths, speeds, etc.) with the same end effector (a fingertip) or even with other end effectors — a phenomenon known as "motor equivalence" — so why is any particular method chosen by the motor system? Generally speaking, this motor redundancy can be viewed as a positive phenomenon that contributes to our adaptability. Nevertheless, humans tend — consciously or not — to move in straight lines when pointing, with a characteristic bell curve of velocity, regardless of the direction, amplitude, or area of space in front of them [42]. Further, when individuals are presented with an unfamiliar motor task they initially move in distinctive ways, but after some practice they move similarly to each other [43]. This regularity in behaviour is in line with modern computational theories of motor control and learning: namely, optimal control.

1.2.1. Optimal Feedback Control Theory

Optimal control, or optimal feedback control, is a computational theory of motor control that centers around the idea of a control scheme or policy [44]. Control policies are essentially a mapping of the motor systems current understanding of the body and environment to motor commands. As discussed above, a near infinite number of control policies can be set to achieve a given task. However, optimal control theory states that the motor system aims to set a control policy that completes the task or maximizes reward while minimizing the cost. The cost to be minimized is thought to be the endpoint variance — that is, the motor system sets a control policy that minimizes the potential error upon task completion on a trial-by-trial basis, maximizing consistency — rather than minimizing energy or force, for example [45]. Movement is therefore controlled by a feedback controller that sets and uses a control policy to dictate how to handle incoming sensory feedback as the movement unfolds. Importantly, the current state of the body is a noisy estimate based on delayed sensory feedback. Computation of a control policy thus requires an internal forward model that predicts the consequences of a motor command on the state of the body based on currently available sensory information [46]. When the feedback controller sends a motor command to the body, an efference copy is also sent to the forward model, allowing it to compare the predicted and actual results and correct course as the movement unfolds — if the movement is not already finished, which can be the case for quick movements. These aspects of a computational model are presented in Figure 1.1 below (a Figure that will be referred to frequently in section 1.2). While the theory might sound intuitive, the predictions that follow are sometimes surprising, yet well supported in the literature [47]. For instance, optimal control predicts that perturbations that are not relevant to completing the task are not corrected for. An example would be bumping one's elbow while reaching for a target: if the hand position has not changed then one can simply maintain the new elbow position and continue with the movement with equal success — thus exploiting the redundancy of the motor system. This prediction has been validated empirically [48]. It is worth noting that control policies are considered to have superseded the concept of an inverse model [39], which was thought to be an internal model that transforms a desired movement trajectory into a motor command. Control policies achieve what an inverse model would while also accounting for how an ongoing movement handles the relevance of incoming feedback (e.g., the elbow bump example above).

Optimal feedback control theory offers a useful framework upon which to understand motor learning. Motor learning may involve forming or updating one of two core components of optimal control theory, or both: a forward model or a control policy. Evidence exists that either can be the case depending on the nature of the task to be learned. Motor control and learning studies often employ adaptation paradigms to investigate motor learning [49]. Adaptation studies have participants perform a task while external perturbations induce errors which are to be corrected for over time. Common experimental paradigms include having participants wear prism goggles that shift the visual field, or force field experiments where participants move toward a target while holding a robotic arm that can be perturbed [50]. Adaptation tends to occur quickly (on the order of minutes) with participant error decreasing exponentially. Eventually performance returns to baseline; that is, performance error returns to that observed without perturbation. Due to a phenomenon known as savings, re-learning a particular perturbation for a second time tends to occur faster. This model can be extended to more complicated situations like multiple targets [51], or randomly varying perturbations [52]. It appears that adaptation occurs in response to prediction errors — that is, the forward model is updated based on the discrepancy between the predicted error and the observed error [53]. In addition to such "model-based" (as in, internal models such as a forward model) learning, error reduction also appears to be driven by "model-free" mechanisms such as use-dependent learning and operant reinforcement [52]. Use-dependent learning simply refers to a bias in a particular direction that occurs after repeating the movement many times. Operant reinforcement refers to a particular movement being associated with successful error-reduction, which may explain the phenomenon of savings. These forms of learning appear to be independent from the forward model [52], suggesting that "model-free" motor learning is supported by other mechanisms such as changes in control policies [54]. While optimal control theory offers a good explanation for what the motor system aims to achieve with movement, how the constructs described (e.g., forward models and control policies) are represented is less clear (see discussion of representational level of analysis in section 1.3 below).

1.2.2. Motor Skill Learning

Motor learning is not restricted to the correction of perturbations but also includes improvements in movement execution beyond baseline performance. Adaptation experiments may fail to reveal such mechanisms since they do not require improvements beyond a return to normal, pre-perturbation movement [55]. Rather, adaptation experiments require a new mapping of movements to goals. In the case of a visual perturbation, a given movement direction results in the end effector (for instance, a finger) reaching a new endpoint in space, and thus correcting this error means changing the movement direction to meet the desired endpoint. The movement itself (i.e., pointing one's finger in a particular direction) is not new, nor does it require improvement. Motor learning can also occur during tasks for which no perturbation exists, and where error occurs because the task is unfamiliar or difficult. Indeed, this is the case for many real-world examples of motor learning such as improving the accuracy of a skill in sports, music, or a trade. Performance is not limited by a baseline of near zero error as in adaptation studies; rather, performance in motor skill learning can be improved over very long periods of time, if not indefinitely [56]. While a clear distinction may prove difficult to make, for the sake of simplicity we will refer to improvements in movement execution above baseline as "motor skill learning", and the improved movement as a "motor skill".

Motor skill learning can be achieved through increases in speed at a given level of accuracy, or improvements in accuracy at a given speed, where the two are related as per Fitts law (discussed above). Motor skill is therefore best operationalized by a speed accuracy function [55,57]. Perfect performance would be consistently accurate task completion at a speed only limited by physical constraints of the body — an unlikely result no matter how long one practices. Note that here speed refers to the speed of the movement itself, and not how long it takes to initiate the movement which may be more relevant to decision making research (see section 1.3.4) and which is also studied using speed-accuracy trade-offs [58]. Motor skill learning is characterized by a slow reduction in trial-to-trial movement variability and an increase in the smoothness of the executed trajectory, with skill generalizing across speeds [55]. Such performance improvements may be due to changes to the control policy, or a refinement of some sort of stored movement representation. Interestingly, it appears that as one becomes more proficient at executing a motor skill — and able to perform accurately at speeds that are faster than sensory feedback delays [59] — feedback-based control becomes less of a contributor to performance, and it seems a feedforward controller executes a planned movement trajectory [60]. This may be what is in fact happening when skills reach Fitts and Posner's autonomous stage of motor learning. Some of these computations may be represented by aspects of the so-called "motor program" (see section 1.3.1 below).

1.2.3. Action Selection, Motivation, Reward & Punishment

Researchers now tend to distinguish between motor skill learning due to improvements in either action selection, action execution, or both, with adaptation comprising both with an emphasis on selection [34,61–64]. Action selection refers to the selection of appropriate movements and where improvements in performance are achieved by learning what to do and when to do it [34]. This includes adaptation paradigms whereby perturbations are linked to appropriate movement responses (e.g., a strategy like "reach slightly to the left rather than straight ahead" to compensate for the perturbation) [64]. Action execution refers to the actual performance of the selected movements and where improvements in performance are achieved via motor skill learning (see section 1.2.2 above)[34,55]. Importantly, consensus is growing that serial reaction time (SRT) tasks are well suited for studying aspects of action selection, particularly learning associations between stimuli and appropriate action choices, and understanding the order of events to predict and prepare future actions [55,61–65], but not motor skill learning associated with improvements in action execution as discussed in the preceding section. As such, SRT tasks are likely more appropriately considered cognitive tasks that are simply indexed by movement (e.g., button pressing) rather than motor tasks themselves [63]. Indeed, given that movement is the only output of the brain it is difficult to imagine a behavioural task that does not involve movement — whether it is a language task that require the vocal cords to speak, or an attention task tracking eye movement — but that doesn't mean we would consider these tasks "motor tasks" per se or that those experiments interrogate motor control or learning. How we define and operationalize phenomenon depend on what we are interested in studying. The work presented in this dissertation will focus on a more specific conceptualization of action execution (discussed above) and motor skill learning (section 1.2.2 above). That said, action selection and cognitive processes play a critical role in the control and learning of movement. Therefore, while a thorough treatment of these topics is outside the scope of this dissertation, a general review will be necessary for providing context. Furthermore, action selection represents an area of overlap between computational / behavioural and algorithmic / representational perspectives and will be discussed in greater detail below, particularly in sections 1.3.3 (Cognitive Processing) and 1.3.4 (Decision Making & Motor Planning).

An important aspect of motor control and learning is motivation, reward and punishment [61,66,67]. Reward and punishment appear to have a complicated effect on action selection, depending on the task, context, and experience of the participant. For instance, the avoidance of punishment is interpreted as a reward signal even if there is a negative value associated with the feedback — that is, it is rewarding if it "wasn't as bad as last time" [68]. Explicit motivation is thought to drive reward seeking behaviour and therefore likely has its effects primarily on action selection [67,69]. Implicit motivation appears to influence action execution; when motivated, participants appear to increase motor "vigor": the speed, amplitude or frequency of a given movement [67,70]. In fact, recent work has shown that motivation by reward can shift the speed-accuracy function independent of learning [71], as though a movement is approached with more skill when it is known to be rewarding. The authors suggested that improved performance was possible by a reward-mediated reduction in noise; that is, by reduction of distractions allowing for more precise movement selection — which comes at a cost to neural resources that may be justified by the potential reward. Perhaps the inverse of this phenomenon explains the sports idiom: “They didn’t want it enough”. As for motor learning, the role of reward and punishment is surprisingly less clear despite decades of sport coaching wisdom [61]. This appears to be due to most experiments on reward and motor learning having been focused on adaptation tasks rather than motor skill learning as conceptualized above, and a general lack of laboratory-based tasks that adequately isolate reward, punishment, action selection and execution. To speculate, it is possible that motor learning involves a combination of associating goals with an expected value, reinforcing specific motor commands, or even improving control over the vigor of a movement [67]. How motivation, reward, and punishment affect motor skill learning is therefore an exciting area of future work.

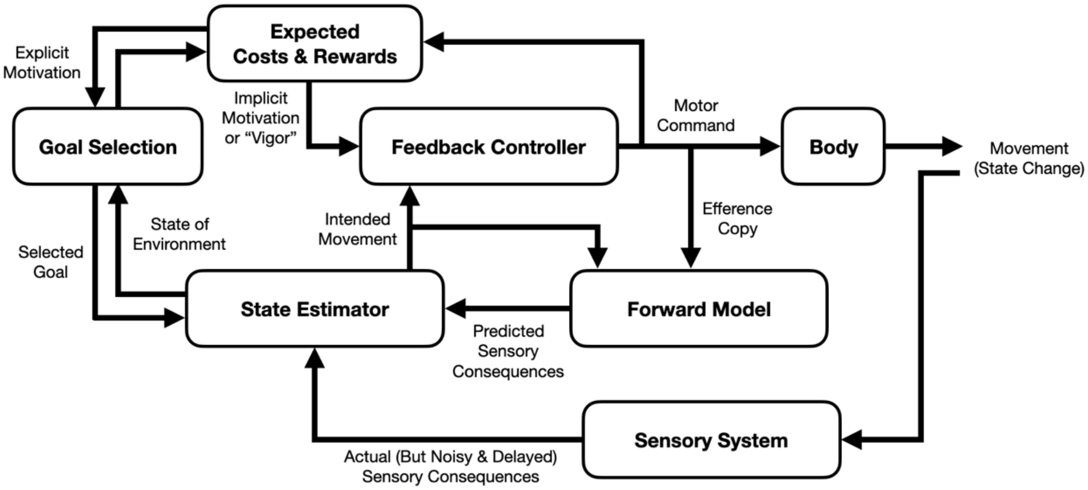

Figure 1.1. A computational model of online motor control. Briefly, goals represent a desired change in state (e.g., position of the body in environment) which is motivated by awareness of the affordances in the environment. The selected goal (i.e., desired state change) is processed by a state estimator to determine the kinematics necessary to achieve the desired state, resulting in an intended movement. Intended movements are transformed into motor commands by a feedback controller that sets an optimal control policy that dictates how to react to incoming feedback while the movement proceeds. Motor commands (whose parameters are influenced by implicit motivation) are sent to the body while an efference copy of these commands are sent to the forward model. Movement creates a change in the state of the body and environment which produces sensory feedback that is noisy (i.e., uncertain) and delayed. Forward models address this by predicting the sensory consequences of this motor command so that corrections can be made in advance. The state estimator compares the predicted and actual sensory consequences of the movement and informs the feedback controller so that motor commands can be adjusted. This process loops until a movement is complete. As will be discussed in section 1.3.4, goals can change mid-movement (a "change of mind"). Note that several relationships (lines and arrows) may exist that are not included for the sake of simplicity. Figure adapted from Shadmehr and Krakauer (2008)[72] and Scott (2016) [73].

1.3. HOW DOES THE MOTOR SYSTEM WORK? REPRESENTATIONAL / ALGORITHMIC LEVEL OF ANALYSIS

Understanding motor control and learning at Marr's algorithmic level of analysis involves studying how the motor system represents and manipulates information to solve problems. The preceding discussion of what happens behaviourally or computationally may allude to answers, but the goal of such a theory is to provide an organizing framework for various experimental observations, and not necessarily to identify how such goals are achieved. For example, how are these purported control policies learned, represented, manipulated, and utilized? These questions are difficult to answer — there is even debate about whether representations exist [74–76] — perhaps even more so than the deeper implementational level of analysis, given that there are tools that measure neural structure and function. There are no tools for reading the “code” that may or may not be represented in the brain. For the most part, the algorithms of the mind must be reverse engineered. As such, many modern motor control and learning experiments manipulate behaviour and observe neural effects, or vice versa (for example using pharmacological, brain stimulation, and in the case of animal studies, lesion techniques), but still speak little to the underlying processes that connect the two. We can see that a specific part of the brain “lights up” when a certain behavioural outcome is observed, but what is that part of the brain doing to drive that outcome? Historically, work on the algorithmic level appears to have been dominated by the field of cognitive psychology. As will be shown in this section and the next, computational and neuroscientific evidence does provide some support for many of the ideas that follow.

1.3.1. Schema Theory & Motor Programs

One of the most influential theories about how a motor skill may be represented in memory was schema theory [77]. Proposed in the 1970’s and cited thousands of times since, schema theory spurred much experimental work on motor skill learning, including what is learned, how it is learned, and how it is applied. Schema theory was an extension of Adams' closed loop theory of motor learning that recognized the importance of having both recall knowledge to perform a learned movement, as well as recognition knowledge to correct the movement with feedback [78]. Schmidt extended this by asserting that while recognition knowledge certainly existed, sensory feedback systems were too slow to alter fast movements. Instead, he proposed that one relied on a generalized motor program that contained all invariant information that characterised a movement (like one's hand signature), which included such information as the sequence of movements, relative timing and relative forces. This generalized motor program could be scaled across other dimensions (speed, size, even the muscles involved; like writing one's signature with one's foot) by assigning parameters from a motor schema — a separate, more specific memory system that stores absolute parameters, the sensory consequences of them, and their associated motor outcomes. It was via manipulation of these so-called schemas that motor learning occurred. Evidence has supported the proposed separation of generalized motor programs and parameters to some degree: generalized motor program learning is enhanced by keeping relative features constant using a blocked practice schedule (keeping to one skill during a practice session; i.e., one generalized motor program at a time) and providing variability through changing parameters; while the recall schema is strengthened through variable practice scheduling (staggering practice with other skills; i.e., multiple generalized motor programs within a single bout of practice), and limiting parameter variability to the parameter of interest (e.g., speed, but keeping size constant) [79]. These results suggest that different practice structures affect different aspects of a motor skill (the generalized motor program or the schema), which may be taken as evidence of their existence.

Schema theory and the notion of a motor program has been challenged for numerous reasons [79–82], including by the original author [83]. Importantly, some aspects of the theory appear to be simply wrong; for example, it appears that while relative timing appears to be invariant in a motor program, relative force is not [83]. What's more, the theory does not account for some important observations about motor behaviour; for instance, the phenomenon of motor equivalence is not well accounted for [83]. Schema theory was also an incomplete theory of motor learning in that it proposed mechanisms by which one learned to scale a generalized motor program, but not how the generalized motor program itself was learned in the first place [83]. Perhaps the most vehement criticism of schema theory has been that of proponents of the dynamical systems theory of motor control and learning that will be described in the next paragraph [80]. In short, dynamical systems theory proponents claim that schema theory does not provide a satisfactory account of rhythmic movement patterns (e.g., walking, crawling, etc.), their change over time, and posits the existence of vague representations (generalized motor programs, schema) that are not necessarily required for observed behaviour [80]. Finally, if one takes a close look at the literature described above, it appears that most experiments utilize SRT tasks and therefore may have less to say about motor execution and motor skill learning as conceptualized above (see section 1.2.2 and 1.2.3).

1.3.2. Dynamical Systems Theory

Dynamical systems theory posits that the regularities observed in the motor system are not programmed but emerge from the intrinsic dynamics of the system [80,82]. That is, when one reaches for an object, joint movement does not occur because of a multitude of specific muscle contractions that are programmed for this task. Rather, a few simple motor commands initiate a movement that unfolds in a coordinated way that is determined by anatomical constraints and reflexive agonist-antagonist contractions that arise from sensory feedback. Changes in movement arise from a change in task constraints; for example, walking faster eventually necessitates a change in the movement pattern to give rise to running, which is even more distinct in quadrupeds such as horses where increasing speed leads to multiple phase transitions from a walk to a trot to a gallop. Research in dynamical systems theory appears to be chiefly concerned with studying these coordinative structures and how they change over time [82]. Proponents of schema theory however point to the fact that, while the dynamical systems perspective offers a fertile theory for understanding movements that are slow enough to benefit from closed-loop sensory feedback, it has difficulty explaining fast skilled movements where studies seem to indicate that muscle contractions unfold in a pre-programmed pattern even when movement is prohibited [83].

To date, researchers appear to generally agree with the existence of a motor program [82]. Such a consensus is based on both neuroscientific and behavioural experiments [82,84] — but none of which negate the relevance of dynamical systems per se. For instance, it's clear that pattern generators (see section 1.4.1 below) exist in the nervous system and that neural activity unfolds in a way that can be modeled mathematically as a dynamical system [85,86]. In fact, one recent study suggests that motor programs are built from "dynamical building blocks" [87] (see section 1.4.3 below). These dynamical building blocks may be similar to the concept of motor primitives and synergies, discussed in more detail below (again see section 1.4.3; see also Figure 1.2 below). In some sense the descriptive features of dynamical systems theory have been integrated into and superseded by optimal feedback control as discussed above [44]. Thus, the "motor program" might be better described with more specific and experimentally tractable concepts such as an internal forward model, a control policy or feedforward controller, and these can include patterned movements as per dynamical systems theory. Nonetheless, dynamical systems theory has had important contributions to our understanding of motor control and the broader mathematical concepts of dynamical systems continue to play an important role today (see section 1.4.3 below).

1.3.3. Cognitive Processing

Cognitive psychology continues to contribute an understanding of motor learning, particularly regarding sequences of simple movements [88]. For instance, Verwey's cognitive framework for sequential motor behaviour posits that sequence execution is controlled by three levels of processing: perceptual, central, and motor. This information processing approach explicitly frames itself as speaking to Marr's algorithmic / representational level [88] (Figure 1.2 below), and to motor sequences where experiments typically utilize SRT tasks. Perceptual processing involves recognizing visual, auditory or proprioceptive stimuli. Central processing involves manipulation of representations (which may include motor programs) and selecting and loading commands into a motor buffer. Motor processing involves executing the movement with or without feedback. The processing that occurs at each stage is interrogated using experiments that manipulate various aspects of the sequence, such as order, or the effectors used to perform them. Within this framework it is thought that perceptual and central processing is effector independent, while motor processing is effector dependent. For example, altering a sequence at the perceptual level (changing the cue from visual to auditory) may cause errors in both hands proportionally, while altering the sequence at the motor level (speed or amplitude of movement) may cause proportionally larger errors in the practiced hand. These so-called transfer studies have led to many fascinating insights about which brain areas are involved in each level of processing [89,90], and where different stages of learning may occur [91].

It is my observation that motor learning research in cognitive psychology appears to evolve largely in parallel with computational theories stated above, with little cross-citation other than both groups associating their constructs to findings in neuroscience. For example, when cognitive psychologists speak about “motor processing”, they may be referring to the same phenomenon as “action execution” as understood in optimal feedback control theory — or perhaps they do not, and the concepts only overlap partially (it is unclear). While the two literatures may appear to be speaking to similar phenomena there are noticeable differences in terminology and methodology. For instance, it appears cognitive psychologists focus on understanding how we learn and produce sequences of simple movements using SRT tasks where sequences of keyboard presses are manipulated in order, frequency, and so on [88]. Behavioural studies in computational work seem to investigate discrete but more complicated movements such as reaching, which allows for more detailed kinematic analysis, and can be modelled mathematically [25]. Such differences are important as inferences made about important concepts can differ significantly by the experimental task used and its complexity [92]. For instance, the impact of reward and punishment differs depending on whether the participant performs a sequencing skill or a motor skill [93]. Authors involved with computational work appear to be increasingly interested in sequence literature as their attention shifts to processes that are “upstream” to execution [62], which may be a signal that the two bodies of work may soon become more integrated. This new line of computational work on sequences likely has much to learn from existing literature from cognitive psychology. In any case, differences in these two perspectives are not easily justified as a focus on different levels of analysis (one group focusing on the computational perspective versus one group focusing on the algorithmic perspective), as the subject matter addressed by each group appears to be overlapping. Notably, researchers who traditionally concern themselves with computational perspectives are making strides in understanding motor planning and decision making in sensorimotor control [94,95] — topics that begin to speak to an algorithmic / representational level of analysis of motor control and learning. Therefore, these two sets of literature appear to be converging from different directions. Given the challenge of reconciling disparate bodies of literature regarding the representational level of analysis, an original figure was created to organize some of the concepts in this chapter and depict their potential overlap (Figure 1.2 below).

1.3.4. Motor Planning & Decision Making

Motor planning is thought to comprise processes that select and specify actions once a goal is already selected [95]. Given that goals can be selected via non-motor processes they are not considered part of motor planning per se. For convenience these stages are discussed as though they occur serially, but the following paragraph will reveal that this is an oversimplification. Once a motor goal is selected motor planning processes determine how the action is to be performed, which means determining what a movement should look like, selecting an action that takes this into account, and specifying the motor commands to achieve it. For simple movements like point-to-point reaching this might require nothing more than setting the control policy (as outlined in the discussion of optimal control theory above; see section 1.2.1) or setting initial conditions (as per dynamical systems theory) and initiating the movement. This is thought to occur quickly, accounting for very little of the reaction time from target cuing to execution. However, if the movement requires a more complicated trajectory — to get around an obstacle, for example — additional planning is required to determine the ideal kinematics, and this has been shown to be costly with respect to reaction time (nearly 100ms in one experiment) [96]. More recent work contends that different plans create different states in the motor areas of the brain, and that plans are in fact what represent separate motor memories [97]. Perhaps a "motor program" is not simply a learned sequence of discrete motor actions but can also be a kinematic trajectory that has been optimized over time, requiring less planning and feedback control as skill increases [60]. Indeed, the popular notion of a motor skill typically does not refer to a well-made decision, but to the grace and precision of a well-executed movement.

Before a movement can be executed or even planned, it must be chosen. As discussed above it appears that the motor system controls movement by minimizing costs and maximizing rewards of a given goal (or a target, as is typical of experiments in motor behaviour), but often a goal has to be selected from many competing candidates. Not surprisingly, when subjects are given a free choice between two targets, they tend to select targets that minimize movement-related costs [98] and maximize reward [99] — suggesting that decision making in action selection may share with, or receive information from, mechanisms of motor control. Surprisingly, however, it appears that before an action is selected, the motor system simultaneously prepares competing movement plans for each potential target [100], and that this is true whether a movement is executed before (go-before-you-know) or after (go-after-you-know) a target is cued [101,102]. One reason for this seems to be that determining the costs of a potential action involves not only assessing the position of a target, but the movement required to reach it — thus the motor system appears to transform visual targets into motor representations ahead of making a final decision and can do this for multiple targets simultaneously [94]. What's more, decisions do not occur at any particular moment but occur continuously over time: for instance, sensory feedback gains that favor a particular target scale linearly as the target becomes clearer [103]. Because of this the motor system appears to be able to "change its mind" — that is, to switch to another target during an already unfolding movement if accumulating information becomes compelling enough to make the new target a superior choice [104]. This happens at such a high speed (15 milliseconds) that it seems the new movement must have been specified in advance and maintained during the action as a contingency plan. Finally, when performing a sequence task, the motor system appears to optimize paths based on the effectors used: for example, if selection is achieved by gazing at a target, the optimal sequence of target-to-target transitions is not the same as when using one's hand to select a target, likely due to the biomechanical cost of distance being higher in the latter case [105]. In conclusion, it appears that action selection and execution are not serial processes, and multiple motor representations can be maintained in the brain simultaneously. This allows the motor system to perform efficiently in unpredictable dynamic environments like those found in the real world.

The interaction between decision making and motor learning is fascinating. Traditionally decision making is thought of as a strictly cognitive process, but improvements to cognitive processing can still drive improvements in motor task performance — that is, improved perceptual processing (e.g., faster recognition of a relevant stimulus [106]), and selection of a more rewarding goal [62] — rather than improvements in motor skill execution. However, recent evidence indicates that as motor learning proceeds, decision making processes make predictions about how motor learning will unfold and therefore select targets that are better suited for the future motor skill [107]. This may imply that motor representations either store expected future errors (based on past errors) or at least can be used by the motor system to generate predictions of future errors. That is, these too supposedly separate processes are in fact aware of one another and work together to converge to optimally achieve a common goal.

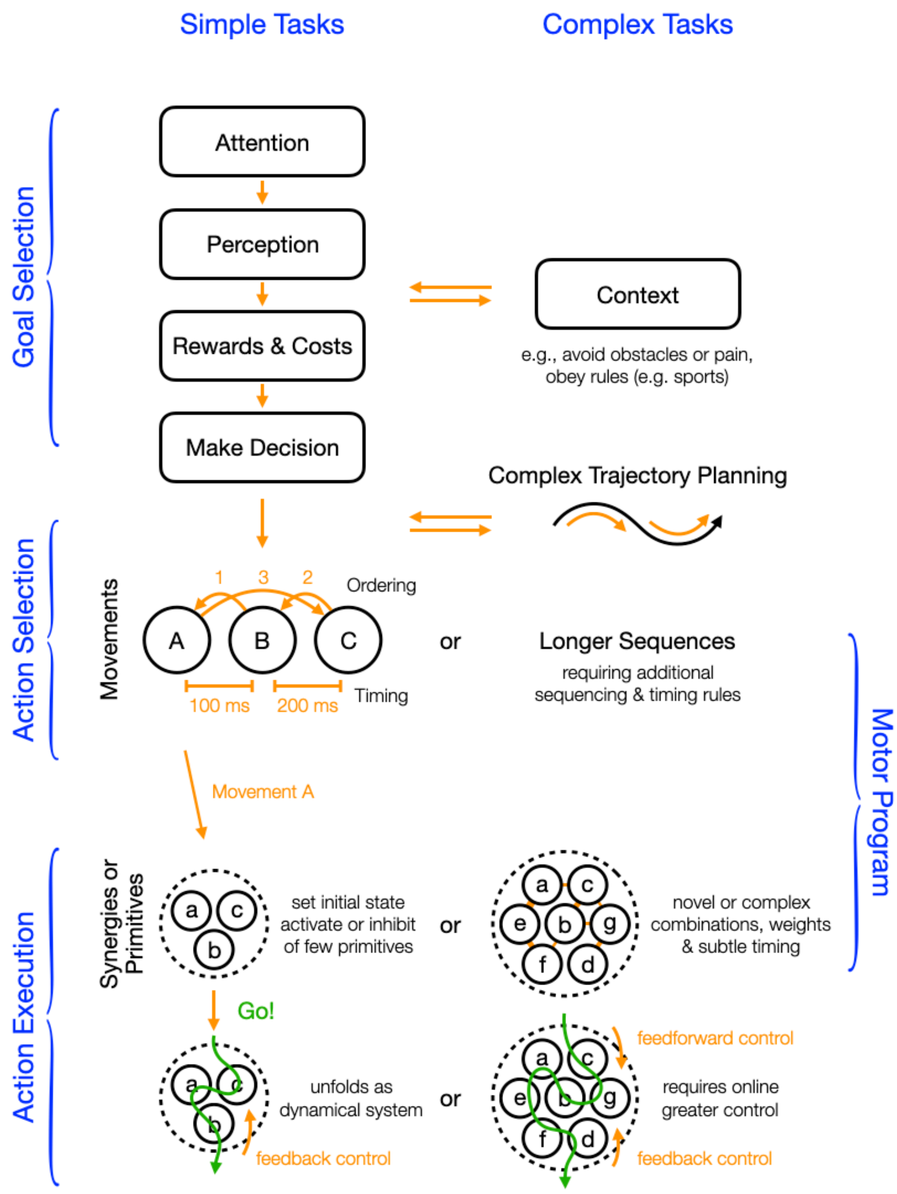

Figure 1.2. A representational model of motor control processes. Briefly, simple tasks require attending to stimuli, perceiving them accurately, determining value and deciding how to respond. More complex tasks may be subject to more context such as rules that constrain choices, or obstacles that require a complex trajectory to avoid. Achieving the goal requires selecting, ordering, and timing a movement sequence, and the longer the sequence, the more complex and challenging the task. For each movement in the sequence, a set of motor primitives or synergies (discussed more in section 1.4.3) that best achieve the goal are activated nearly simultaneously. More complex movements require a greater number of primitives with greater interdependence (more subtle weightings and timing). Movement then unfolds as a dynamical system using these building blocks. Adapted from several figures from Giszter 2015 [108], Verwey et al. 2015 [88], and Wong et al. 2015 [95].

1.4. WHAT IS THE MOTOR SYSTEM? NEUROSCIENTIFIC / IMPLEMENTATIONAL LEVEL OF ANALYSIS

The physical substrates comprising the motor system are distributed throughout the body. While the nervous system acts upon the musculoskeletal system to produce movement, this relationship is not unidirectional. This is evidenced by the critical role of sensory feedback in movement. While a thorough discussion of the neuroscience of movement extends beyond the nervous system itself, the scope of this dissertation will be limited to the nervous system. This review will largely take a bottom-up approach, initially discussing the peripheral nervous system and progressing centrally, but diverging from this approach where appropriate. When discussing voluntary movement this may seem unintuitive as information seems to flow from identifying a goal, through the motor system, and then to achieving the goal with the body. However, it is this writer's opinion that when discussing motor control, it is helpful to know "what" is being controlled as it is critical to the problem being solved by the controlling systems.

1.4.1. The Spinal Cord & Peripheral Nervous System

A significant portion of cellular motor neuroscience has developed by studying reflexes in the peripheral nervous system. Seminal work on reflexes dates back over a century and principally applies to spinal reflexes. While volitional movement is a process that is initiated with intention, reflexes are generally understood as being capable of initiating movement in the absence of input from the brain [109]. Instead, reflexes typically operate in reaction to an external stimulus. However, reflexive movements are still capable of being driven even when sensory input is blocked [110]. This demonstrates the intrinsic nature of spinal reflexes but does not imply that they act alone in the motor system. On the contrary, spinal reflexes receive a variety of descending (i.e., from the brain) inputs [111], making the distinction between conscious and unconscious movement a difficult one to make [35]. Caveats aside, the spinal cord alone is capable of complex computations. For instance, neural networks known as central pattern generators that can integrate sensory information to coordinate complicated movements like walking without the need for descending input [85]. Spinal circuits receive a wide variety of sensory inputs from various peripheral receptors in the muscles, joints, and skin [112]. The output of the spinal cord is ultimately the activation of muscle tissue through motor neurons, of which there are now known to be at least seven different types [113]. This complexity of spinal circuits can be leveraged to drive motor learning itself [5] — for example, animals that have had their spinal cord cut are still capable of learning to walk on a treadmill as long as they are able to receive sensory input during training [114]. This type of learning is likely simple: regulating muscle activations in light of sensory inputs (the training) until some level of regularity persists. This may be the neural basis of use-dependent learning discussed above (see section 1.2.1 above). While simple, the implications are substantial for rehabilitation from spinal cord injury.

1.4.2. Subcortical Structures

The spinal cord receives descending inputs from several cortical and subcortical structures [111]. The path from the cortex (discussed in more detail in the next two sections) to the spinal cord consists of several tracts that typically make a stop in the brain stem, but some cortical neurons appear to directly innervate motor neurons in the spinal cord [115]. These direct projections appear to be involved in fine motor control such as precise finger movements and appears to be especially present in humans compared to other species [116]. Interestingly, though limited to control of the whole hand rather than more dextrous movements, the brainstem is a candidate site for the storage of planned movements [117,118]. Animal models have also demonstrated that subcortical structures are capable of executing learned motor skills, but that the motor cortex is necessary for learning [119]. It appears that while control from higher brain structures may be necessary to drive motor learning in these regions, they are nonetheless capable of storing motor representations. These subcortical structures may be ideal candidates for the storage of highly automated motor skills that are driven by a feedforward controller (see section 1.2.2 above) [60] — but not exclusively so (see section 1.4.3 below) [120].

The cerebellum is a subcortical structure highly implicated in motor control and learning [2,121,122]. It is thought to be responsible for implementing the forward model and is associated with motor adaptation [2,72,123,124] (Figure 1.3). The cerebellum appears to send predictions of the sensory consequences of movement to the parietal cortex (discussed below) where it may be combined with processed sensory feedback to compute prediction error [125]. However, it is not clear that the cerebellum is a site of storage for motor learning, and evidence suggests the motor cortex (discussed below) retains the information "learned" by the cerebellum [126].

The basal ganglia, which refers to a set of subcortical structures that appear to form a related circuit, has been implicated in several aspects of motor control and motor skill learning [2,67]. For instance, the basal ganglia appear to have a role in motivation, action selection and sequencing (see section 1.2.3 above) [67]. More recently, it has been proposed that many experimental observations may be more succinctly explained by the idea that the basal ganglia are involved in both explicit and implicit motivation, which respectively drive reward-seeking behaviour and the “vigor” (e.g., the speed, amplitude, or frequency) of a movement [67,69,70]. The basal ganglia are therefore an ideal candidate site responsible for computing the cost and reward structure of movement (as per Optimal Control Theory; section 1.2.1 above; Figure 1.3 below) [72], and may be involved in modulating movement parameters (as per schema theory; section 1.3.1 above) by applying motivational effects [67]. Neuroimaging work has shown that successful reward attainment is associated with shifts in brain activity from the anterior insula to the ventral striatum [68] — the primary input to the basal ganglia [67].

1.4.3. The Motor Cortex, Premotor & Supplementary Motor Areas

The primary motor cortex has a long and storied history in the neuroscience of movement. The seminal work by Penfield and Boldrey introduced the concept of “motor maps” whereby the primary motor cortex appeared to encode a map of bodily movements as revealed by direct electrical stimulation [127]. Decades of both animal and human work have contributed to more nuanced understandings of the motor cortex [86,128–131]. It appears that motor maps are not of individual body parts or muscles, but of species relevant “action maps” (e.g., reaching, grasping) [131], and the motor cortex exerts control by both eliciting and inhibiting these movement [130]. Motor cortex appears to achieve this control by activating (and inhibiting) combinations of muscle “synergies” or “motor primitives” that can be combined to form novel movements as though selecting letters from a limited alphabet to create a seemingly infinite vocabulary [108,128]. Indeed, computational models of learning based on optimal control theory are aligned with this idea [51]. The activity of these neural populations demonstrate complex patterns that are readily modelled using a dynamical systems perspective [86]. Motor cortex neuroscience may therefore resolve some theoretical debates: for instance, motor programs (section 1.3.1) or plans (section 1.3.4) may represent an organization of motor primitives that are sequenced — with more overlapping co-activation in "discrete" or "continuous sequence" movements compared to "discretely sequenced" movements — which once activated unfold as a dynamical system (section 1.3.2) while utilizing feedback according to a control policy (section 1.2.1). Control policies themselves may be encoded in the motor cortex [72] (Figure 1.3). Importantly, recent evidence suggests that movement sequences that are less continuous and overlapping, and more discrete in their ordering (see section 1.3.3 above), are unlikely to be represented in primary motor cortex and appear to be more widely distributed [63,65]. Importantly, primary motor cortex appears to be the site of storage for learned motor skills (as defined in section 1.2.2) in humans [120] — potentially through the strengthening of specific patterns of primitives at the cellular level (i.e., formation of dendritic spines) [132]. While the primary motor cortex clearly plays an important role in motor learning, it appears to be limited to controlling movements that are being executed. To oversimplify, the primary motor cortex appears to simply do the work that it is told to.

Premotor cortices appear to have an important role in translating movement instructions into action [133]. That is, premotor cortex receives visuospatial information from the posterior parietal cortex (PPC) [134], processes a movement sequence to derive both spatial and temporal features [135], can use this information to aid in goal selection [136], and perform complex movements [65,133,135]. Premotor cortex has been implicated in learning of motor sequences [65,133], as well as discrete motor skills along with the primary motor cortex [120]. The planning and control of movement sequences has also been associated with the supplementary motor area (SMA) [137], which is strongly connected to parietal, cingulate, and primary motor cortices and even projects directly to the spinal cord [111,138]. The most anterior region of the SMA, known as the preSMA, appears to be active during sequence learning [139] and is more strongly connected with prefrontal cortex [138]. This supports the notion that the SMA is involved more in movement control whereas the preSMA is more involved in movement planning. Overall, premotor and supplementary motor cortices appear to operate at a higher level of abstraction than the primary motor cortex and are critical for complex motor behaviour.

1.4.4. Parietal & Frontal Cortex

Parietal cortex has been implicated in several aspects of motor control and learning. The anterior region of the parietal cortex includes the somatosensory cortex which processes incoming sensory information. Given the critical role of sensory feedback in motor control, it is not surprising that the somatosensory cortex appears to play a critical role in updating internal models during adaptation tasks and has even been hypothesized to store internal models [140], though this is not entirely clear [64]. The PPC is known as an area of spatial processing and sensory integration [141,142], is involved in attention and selection of motor tasks (see section 1.2.3 above) [143–145], has been implicated in the storage of motor representations [146], and appears to be the source of an intention to move (Figure 1.3) [147–149]. The parietal cortex appears to work together with premotor regions to aid in goal selection [136]. Furthermore, the PPC has been hypothesized to be responsible for planning more complex kinematic movement trajectories (see section 1.3.4 above), perhaps by formulating where the end effector must travel to achieve the goal [95,96,150]. In particular, the superior parietal lobule (SPL) appears to integrate visual and somatosensory information and project to the premotor cortex [7]. The inferior parietal lobule (IPL) appears to be necessary for attending to and encoding implicit aspects of motor sequence learning (see 1.3.3 above) [91,142]. Given that the parietal cortex also receives input from the cerebellum [125], it appears to be an ideal candidate for processing sensory prediction error (as per optimal control theory; section 1.2.1) [72].

Neuroimaging studies frequently show activation in prefrontal cortex during motor tasks [7]. The role the frontal cortex plays in motor control is principally in decision making and planning future actions, rather than in the control of an ongoing action [151,152]. While prefrontal cortex does not appear directly involved in movement execution, neural activity in this region appears to be responsible for changes-of-mind (see section 1.3.4 above) [153]. This demonstrates the considerable influence executive function can have on motor control across time scales — from making complicated decisions about what actions to perform well in advance of their performance, to exerting conscious control in the middle of an ongoing movement.

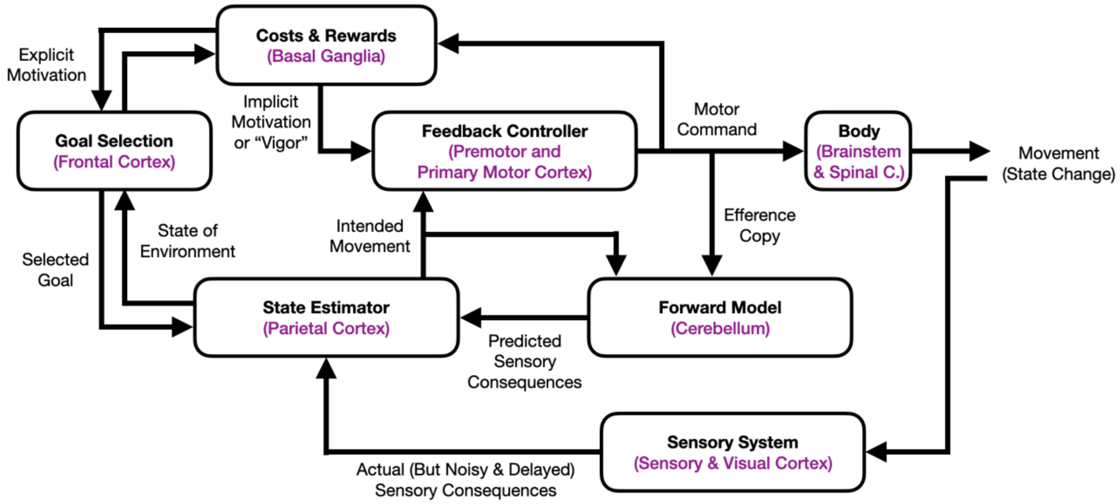

Figure 1.3. A Computational Neuroanatomy of Online Motor Control. An extension of Figure 1.1, mapping neuroanatomical regions to computations they likely perform. Note that this figure represents online control of an ongoing movement and is not intended to describe where changes occur to drive learning and store memory or skill (though this figure may provide insights). Adapted from Shadmehr and Krakauer (2008) [72].

1.5. MOTOR IMAGERY

The preceding literature review covered the topic of motor learning entirely within the context of overt movement performance. But as mentioned in the opening paragraph of this dissertation, motor learning appears to be possible in the absence of movement and therefore absent any sensory feedback [16], even when that movement has never been experienced before — though notably, these previous studies frequently utilize SRT tasks [154], and studies that utilize more complex tasks include pre-tests that afford participants with an experience of the overt movement prior to imagery [155]. Those issues aside, given the critical role feedback appears to play in motor learning (in particular, see section 1.2.1) [4], motor imagery is theoretically interesting and may have important implications for neurological rehabilitation where patients typically have limited movement [13–15]. Unfortunately, the motor imagery literature represents a small fraction of overall motor control and learning literature and is not as well understood. Critical issues that remain a matter of debate include whether motor imagery engages aspects of the motor system involved in overt execution or is instead a perceptual or cognitive process [27,156], and what types of motor learning (e.g., sequence learning, adaptation, or motor skill learning; see sections 1.2.2 and 1.2.3 above) motor imagery is capable of driving. Here I will review two opposing viewpoints of motor imagery before reviewing evidence of motor learning via motor imagery and the possible mechanisms underlying this learning considering these viewpoints. Finally, I will make the case that these differing views of motor imagery-based learning may be at least partially resolved by carefully considering the experimental task used. This context motivates the three experiments presented in this dissertation.

1.5.1. Motor Simulation & Functional Equivalence

Motor simulation theory has been an influential theory of motor imagery for the last two decades and remains so to date [27,157]. Motor simulation theory proposes that motor imagery involves much of the same perceptual, cognitive, and overall planning processes as overt movement, but diverges once reaching the action execution stage. The performance of motor imagery involves a simulation of the prepared movement such that it unfolds covertly but in the same way it would if it were being executed overtly. Here simulation refers to a person's covert performance of the movement, as opposed to simply imagining what such a movement might look like if someone else did it or forming an abstract representation of the movement without performing it (like having a map of a path but not walking through it). The simulation thus gives rise to a mental image of the movement being executed by the imaginer. Motor simulation theory was built on behavioural data showing that the timing of imagined movement aligns well with the timing of the same overt movement, and neurophysiological data demonstrating considerable overlap between imagined and overt movements including, at the time, the primary motor cortex [11,12,157]. More recent but highly related theories include so-called emulation theory which supposes that both visual and somatosensory outcomes of the simulated movement are generated and available to the motor system [158,159]. Given that overt movement also involves simulated movement by way of forward models [46], motor simulation theory supposes that motor imagery is functionally equivalent to overt movement with the exception that overt movement is inhibited [27,157].

While motor simulation theory remains an influential theory of motor imagery, many of its particulars have been scrutinized. Critically, since the theory was first proposed further neuroimaging studies have shown that the primary motor cortex does not appear to be consistently activated during motor imagery [20,23,27,160]. Neuroimaging studies (see Figure 1.4 below) have also demonstrated numerous subtle but important differences, where motor imagery is associated with greater activation in frontal regions [23], greater activation in preSMA [161], greater activation in PPC [20,161,162], greater activation in caudal cerebellum [23,162], and greater activity in the rostral basal ganglia [20,23,161]. Given the preceding review of the neuroscientific basis of motor learning, these neuroimaging results suggest greater cognitive involvement in motor imagery and potentially fewer motor processes. Indeed, behavioural evidence suggests that motor imagery is more reliant on perceptual learning than motor learning [26] and is disrupted by inhibitory brain stimulation to the IPL but not the primary motor cortex [163,164] (though these experiments used an SRT task). What's more, the time it takes to complete an imagined movement is readily disrupted by cognitive interference [156]. Together these results question the idea of functional equivalence. However, this does not prove that motor simulation does not occur, as simulation may be represented and implemented in several ways depending on the task. For example, the movement can be simulated, sensory feedback can be simulated, movement outcomes can be simulated (e.g., ending position, location of an object) rather the movement itself, and so on.

1.5.2. Cognitive Theories of Motor Imagery

Opposing theories of motor imagery have proposed that, beyond the planning stages, motor imagery does not simulate a newly specified movement to estimate sensory outcomes, but rather substitutes the lack of sensory feedback by recalling sensory outcomes of past movements from memory [165,166]. These theories suppose that motor imagery is highly cognitive in nature and involve searching procedural memory for past movement representations suitable for the task — which is particularly challenging for a novel movement where the process will rely on finding past movements or movement components that represent a best fit [166]. In these theories, aspects of the motor system involved in overt movement execution are not utilized by motor imagery. Authors typically point to the fact that motor imagery has an imperfect overlap with overt movement in neuroimaging studies (see Figure 1.4 below), particularly an inconsistent or absent activation of primary motor cortex [23,166]. Indeed, studies demonstrating motor learning via motor imagery often include overt pre-tests prior to imagery that afford the participant with a motor memory to rehearse [155,167]. Furthermore, studies of motor imagery frequently employ SRT tasks that can be argued are primarily cognitive tasks (see section 1.2.3 above) [16,27].

One of the more recent theories of motor imagery is the motor-cognitive model [156]. Much like motor simulation theory, the motor-cognitive model proposes that the planning stages of motor imagery are identical to those of overt movement. However, once the execution stage is reached the motor-cognitive model proposes that motor imagery diverges from overt movement. Where overt movement then relies on largely automated and feedback driven processes to guide execution, imagery instead becomes an executive process that does not utilize the motor system. Specifically, motor imagery involves creating an abstract representation or image of the movement, and rather than simulating its execution, involves elaborating on this representation. Thus, motor imagery is an executive process that is more difficult when the movement is more complex, requires greater cognitive resources and is therefore more easily disrupted by interference tasks than overt movement. Glover and Baran cite existing evidence and present their own in support of this theory [156].

While the motor-cognitive model offers a compelling alternative to motor simulation theory, it is important to note important challenges that it faces. First, by the original authors' own admission the motor-cognitive model offers no explanation for the potential use of forward models during motor imagery [158]. This is critical given that a recently published report has demonstrated compelling evidence for the existence of forward models in motor imagery [168]. What's more, while neuroimaging studies support an increased activation in frontal regions during motor imagery, frontal cortex activation is not exclusive to imagery and is also present during overt movement [23]. The motor-cognitive model also predicts increased visuo-perceptual and ventral stream activation, which has not been consistently demonstrated in neuroimaging meta-analyses (see Figure 1.4 below) [23]. Overall, this challenges the motor-cognitive model and cognitive accounts of motor imagery generally.

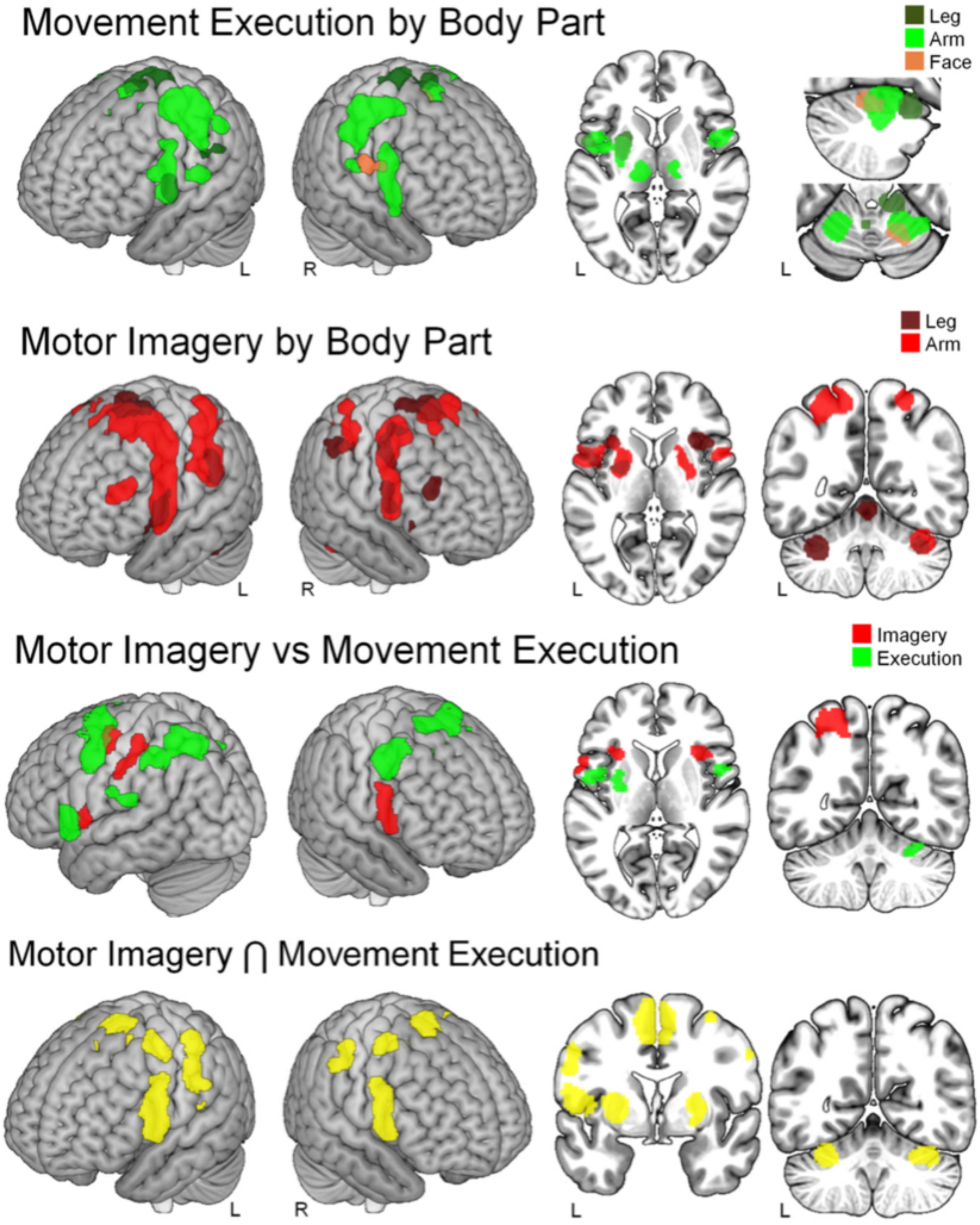

Figure 1.4. Results of a recent meta-analysis of neuroimaging studies demonstrating brain regions involved in motor execution (overt movement) and motor imagery. From top to bottom: activation by body part during overt movement, activation by body part during motor imagery, activation unique to each modality, and finally activation similar between each modality (∩ refers to "intersection" or "conjunction"). Taken from Hardwick et al. 2018 [23].

1.5.3. Evidence of Motor Learning via Motor Imagery

The extent to which motor imagery can drive motor learning remains an open question. That is, what aspects of motor control (see representational summary Figure 1.2) are capable of being improved upon via imagery-based practice, and by how much? Motor learning via motor imagery is almost certainly not the same as the learning that occurs via overt practice. This is clear given a widely replicated difference in the magnitude of learning via motor imagery-based practice compared to overt practice [155,169–171]. However, this difference in efficacy has subtleties that may provide insights as to how the two methods of practice differ. For instance, Kraeutner et al. (2020) had participants train a dart throwing task via either overt or imagery-based practice across five days with pre- and post-training tests as well as a 24-hour retention test [170]. One of the benefits of a dart throwing task is that performance can be operationalized in several ways, including accuracy (e.g., the distance of dart from target) and consistency (e.g., variability in performance across trials), which are thought to speak to different levels of encoding. Specifically, accuracy is thought to be effector dependent (encoded at the level of the specific part of the body performing the movement) and consistency is thought to be effector independent (encoded at the level of task goals, prior to a transformation of kinematics to dynamics) [172]. The results demonstrated that imagery-based practice was capable of driving improvement in consistency but not accuracy, while overt practice led to considerable improvements in both (Figure 1.5). These results suggest that motor imagery has a greater effect on effector independent (e.g., action selection) processes that are upstream to execution, and potentially little to no effect on execution accuracy [170,172]. Interestingly, Ruffino et al. (2021) demonstrated slightly different results demonstrating that imagery-based practice led to similar performance improvements as overt practice, but only after a consolidation period 6 hours post-training [169]. That is, overt practice led to immediate performance improvements, but motor imagery required a passage of time (see Figure 1.6). Importantly, this study had participants perform a task focused on action execution and assessed motor skill via changes in the speed accuracy function. Both groups demonstrated a similar gain in performance again at a 24-hour follow up test. These results again demonstrate that imagery-based practice and overt practice are likely driven by different processes.

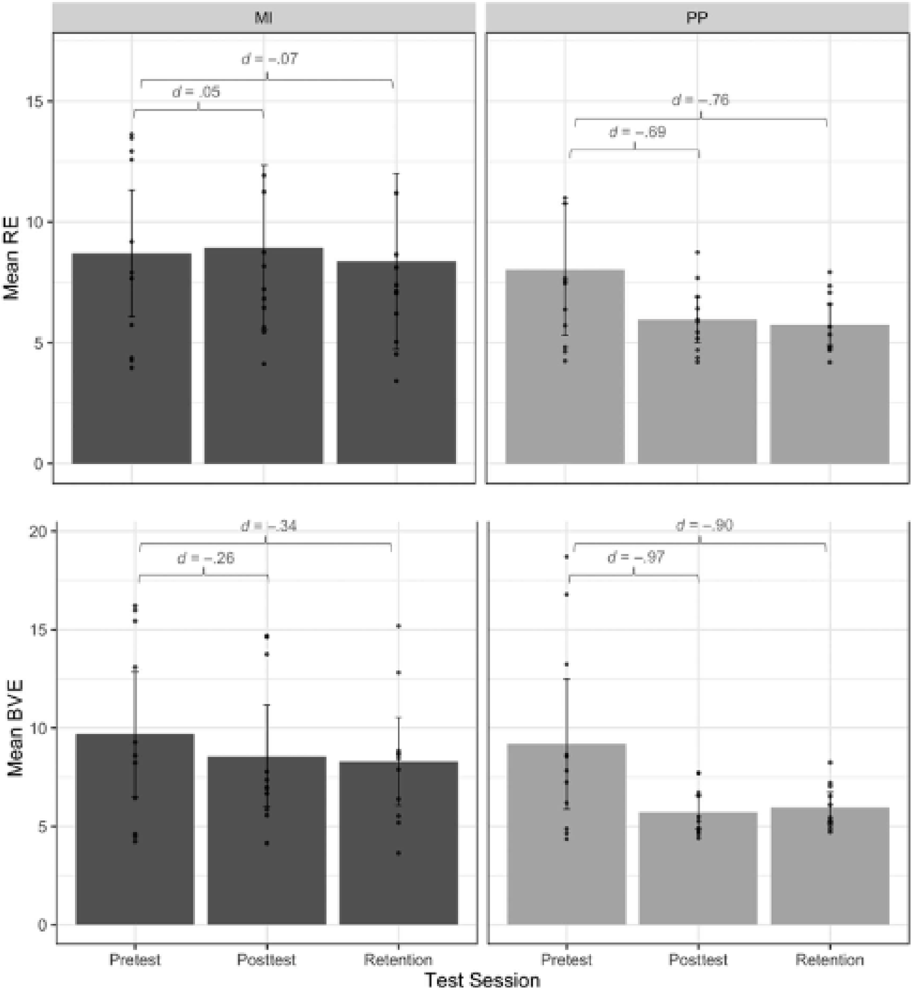

Figure 1.5. Changes in performance via imagery-based practice (MI) and overt practice (here referred to as physical practice, or PP) on a dart throwing task. Two performance measures were assessed: radial error (RE), a measure of accuracy, and bivariate variable error (BVE), a measure of consistency. Effect sizes shown as Cohen's *d*. In both measures, PP outperformed MI. MI only demonstrated significant improvement in BVE, suggesting that MI drives effector independent learning but not effector dependent. Taken from Kraeutner et al. (2020)[170].

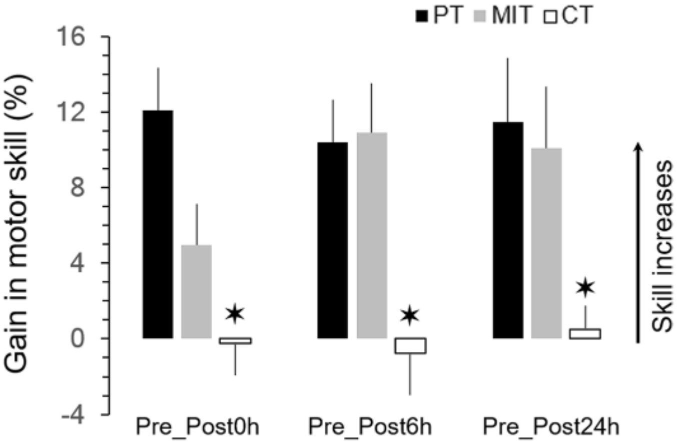

Figure 1.6. Percentage gains in motor skill in a sequence reaching task. Motor skill was defined by a speed accuracy function and therefore representing a reduction of error controlling for speed. Figure demonstrates motor skill immediately after training (Pre_Post0h), 6 hours later (Pre_Post6h), and 24 hours later (Pre_Post24h), for physical (overt) training (PT), motor imagery training (MIT) and control training (CT; no training). PT led to immediate improvements that were superior to MIT, but gains increased in the MIT group while the PT group did not. In this study, imagery-based practice was equally effective compared to overt practice after some time had passed. Taken from Ruffino et al. (2021) [169].

That Ruffino et al. demonstrated considerable learning compared to the results published by Kraeutner et al. is likely driven by differences in the experimental tasks. First, regardless of participant experience with the sport of dart throwing, the task involves highly familiar reaching and throwing motions and improvements are likely driven by a combination of changes to action selection and much more specific changes to action execution. That is, in some respects dart throwing is like an adaptation task where there is a focus on error reduction over time which can be achieved by biasing the throwing movement toward a different target (e.g., “aim higher and slightly to the left”; a form of action selection) while never changing movement kinematics — but kinematics do change during dart throw skill learning [172]. This change in kinematics may be due to a combination (that is difficult to dissociate) of the kinematic changes that follow from altering the selected action — aiming higher obviously alters movement kinematics of the throwing motion — in addition to subtle motor skill improvements at the level of action execution. I contend that improvements in the execution of dart throwing is slow and requires substantial practice, and given that the changes are subtle, relies far more on actual sensory feedback that is not afforded by imagery-based practice. More novel motor skills like that deployed by Ruffino et al. are likely more amenable to imagery-based practice given that action execution can improve materially via processes that do not require the precision of sensory feedback, like motor planning and the creation of novel primitive combinations and/or control policies (see representational figure 1.2 above). However, had Ruffino et al. extended their study from a single day of training to several days, it is likely that overt practice would have led to a greater improvement in skill compared to imagery-based practice.

While less familiar movements may be more amenable to imagery-based practice, some have suggested that prior overt experience is required for motor imagery-based learning and that imagery-based practice cannot drive learning of truly novel motor skills. Mulder et al. (2004) provided evidence in favor of this conjecture by having participants practice for two days, mentally or overtly, a movement the authors considered truly novel [173]. Participants were asked to abduct their big toe without moving their other toes, and if participants were unable to perform this movement at all (zero degrees of abduction) it was considered totally novel. Participants were therefore grouped into four groups at baseline: an “absolute zero” group and an “already doing it” group, and each of those groups further subdivided into overt and imagery-based practice groups. The absolute zero groups demonstrated improved performance via overt practice but not imagery-based practice, but the already doing it groups improved performance via both overt and imagery-based practice. The authors conclude that this demonstrates that motor imagery requires a prior representation of the motor skill, and that learning cannot occur without it. However, there are several issues with this study. First, it is not clear whether performance in this task is due to a lack of familiarity compared to a lack of general flexibility and this was not accounted for. Second, a closer inspection of their results raises questions about the statistical power supporting their inferences. Importantly, the absolute zero imagery group in fact did improve in performance, while a separate no-practice control group did not. In fact, both imagery groups demonstrated the same effect size in performance improvement (Cohen's *d* of 0.45) and differed principally in their baseline measurements. The fact that the absolute zero group did not reach statistical significance is likely due to a lack of statistical power given the small sample size (14 participants). This study should be replicated with either more participants, more sessions, or both. In a review article by Olsson and Nyberg (2010) the case is made that motor imagery requires previous experience to drive motor learning. However, the authors principally cite their own and other neuroimaging studies that demonstrate differences in motor imagery associated brain activity between expert athletes and novices, where the imagery of a sports skill by experienced athletes is associated with activity in motor regions such as SMA, PMA, and cerebellum, while imagery in novices is associated with activity in parietal, occipital and temporal cortex [174,175]. The authors use these differences as a basis for the claim that functional equivalence between imagery and overt execution isn't achieved unless there is a stored representation of the movement. However, these studies used neuroimaging techniques that preclude the possibility of performing those athletic skills overtly (e.g., fMRI), and therefore these results may have less to do with differences between imagined and overt movement and more to do with expertise [176]. Therefore, these results should not be taken to imply that previous experience is necessary to drive motor learning via imagery. Finally, more recent evidence from Kraeutner et al. (2015) has demonstrated that indeed motor learning appears to be possible via imagery-based practice, even in the absence of prior overt experience [154]. Motor imagery studies typically involve an overt movement pre-test to determine baseline movement prior to a training via either imagery-based or overt practice. Such a pre-test was not included in the study by Kraeutner et al. and therefore performance improvements in the imagery group could not be attributed to prior overt experience. The authors demonstrate that motor learning of a novel motor sequence is possible via imagery-based practice. However, given that this study utilized a SRT task the results may demonstrate that improvements in performance are principally due to changes in action selection processes, rather than improvements in the quality of motor execution. Indeed, keyboard pressing tasks have very limited room for improvement in action execution. Therefore, it remains unclear whether motor imagery can drive improvements in action execution for a novel motor skill.

If it were possible for imagery-based practice to drive novel motor skill learning (as conceptualized in section 1.2.2), how might this be possible? While it may be true that, as the motor-cognitive model supposes, motor imagery requires greater cognitive control than overt movement, I believe an extended version of motor simulation theory provides the most reasonable explanation [27,158]. Motor skill learning is likely driven by refinements in the control policy and forward models utilized by the skill (see section 1.2.1 for more detail). If motor imagery is indeed capable of utilizing these components of the motor system, then skill learning may proceed. Indeed, Kilteni et al. (2018) recently demonstrated that motor imagery involves the use of forward models to generate predictions of the sensory consequences of a movement [168]. Given that the computational models of motor control suppose that forward models arise from motor commands that are generated by a feedback control policy (see Figure 1.1 above), this implies that motor imagery is also capable of creating a control policy. Indeed, an animal study utilizing brain-computer interfaces implanted in the pre-motor and primary motor cortex [177], as well as a human study using an adaptation task [171], has demonstrated evidence that imagery can set similar initial neural states in the motor cortex (see section 1.4.3 above) and that this transfers to improvement in overt movement. This latter line of evidence suggests a potential role of primary motor cortex in imagery-based motor skill learning despite the region appearing inactive. That is, perhaps motor simulation produces an input to the motor cortex to train skills, even in the absence of motor cortex activity — to use an imperfect analogy, it may be that the engine is running but the brakes are on. Here motor simulation can be thought of as an alternative to sending a motor command with an efference copy to forward models — that is, the control policy is formed as usual, but the motor command is then simulated to produce an efferent copy for forward model processing. Alternatively, the motor command is generated as usual but while the efference copy is free to proceed to the forward model, the motor command is inhibited before descending to the spinal cord. Either way, learning is then driven not by a comparison between the predicted effects of the motor command and the observed effects, but instead by a comparison between the predicted effects and the intended effects of the motor command (see Figure 1.7) [178].

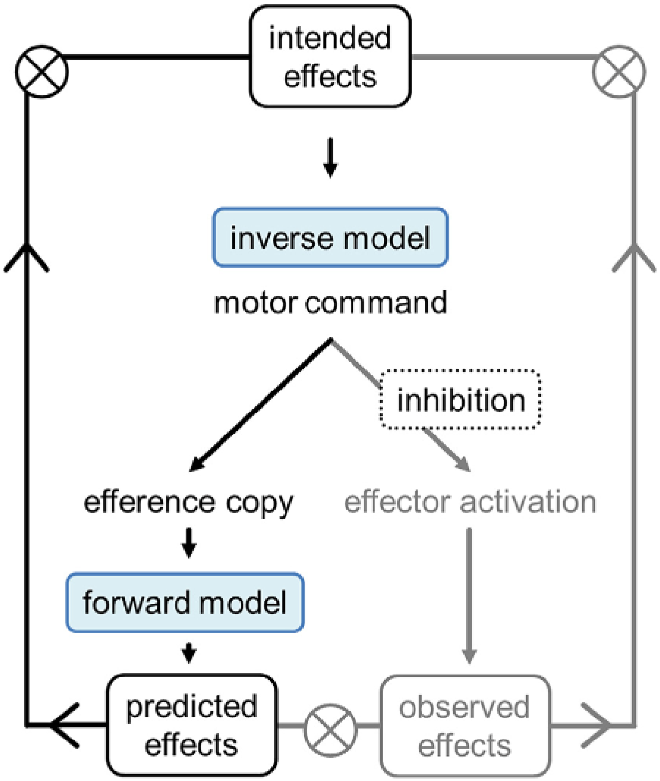

Figure 1.7. A computational model of motor imagery. Motor imagery involves the generation of a motor command with an efference copy used for forward modelling, giving rise to predicted movement effects. Given that movement does not occur, there are no observed effects to compare to the predicted effects. However, predicted effects can be compared to the intended effects of the movement. Taken from Dahm and Rieger (2019) [178].

In conclusion, it has been demonstrated that motor imagery can drive motor learning, broadly defined — but to a lesser degree and potentially to different aspects of motor control than overt movement. That is, tasks that focus on action selection processes are readily learned via motor imagery, which is not surprising given that most theories of motor imagery seem to recognize a strong similarity between the planning stages of imagery and overt movement. However, there has not been convincing evidence that motor imagery can drive learning of a novel action execution skill. Given that there appears to be mechanisms by which this may occur, this appears to be an important gap in the literature. Demonstrating novel motor skill learning via motor imagery would provide support for action simulation theories (though doesn't necessarily rule out the validity of cognitive processing models) and would increase confidence in its practical applications.

1.5.4. Moving Forward by Considering Experimental Tasks

This literature review has highlighted the importance of experimental design in motor control and learning research. Different experimental tasks challenge participants in different ways depending on the task demands and how performance and learning is measured. For instance, sequence tasks likely speak largely to cognitive processing, goal selection and action selection (see sections 1.2.3 and 1.3.3), adaptation tasks speak primarily to action selection (see section 1.2.3), and action execution is best investigated using tasks that focus on the quality of movement (e.g., measure performance using a speed-accuracy function; see section 1.2.2 above) [64]. This attempt to "carve nature at its joints" is not meant to devalue any experimental paradigm or result — all these aspects of motor learning are important in the real world, and the selection of experimental task should be driven by the purpose of the experiment.

However, it appears that the most contentious questions in motor imagery research have not been investigated using the most appropriate experimental tasks. Note for example that where motor simulation theory and the motor-cognitive model disagree is not at the action selection phase but the action execution stage. Yet there have been very few motor imagery experiments that measure performance and learning by focusing on the quality of action execution by measuring a change in the speed accuracy function [169], and to this author's knowledge none that explicitly investigate whether the execution stage of motor imagery involves a simulation or an executive process. This is of critical importance for both theoretical and applied research in motor imagery. For instance, motor imagery-based practice is known to be less effective than overt practice [26,154,169,172]. This may imply that motor imagery only affects certain types of motor learning, and perhaps does not improve aspects of performance that a practitioner cares about, or in the case of neurological rehabilitation, requires depending on the nature of their impairment. Indeed, imagery has been accused of representing perceptual learning rather than motor learning for decades [166], and continues to be compared with motor planning (but not execution) despite recent evidence suggesting that imagery differs from overt movement at the motor planning stage as well [171].

1.6. OVERVIEW OF THESIS CHAPTERS

The experiments presented in this dissertation therefore aimed to investigate whether motor imagery is capable of driving motor skill learning of action execution, and if so, investigate what the underlying mechanisms might be. This involved devising a novel experimental task that allowed for investigating the effects of both overt practice and motor imagery-based practice on the execution of a complex motor skill. Performance was operationalized using a speed accuracy function where learning was defined as changes (i.e., a "shift") in the function. The purpose of the first experiment was to determine whether novel motor skill learning is indeed possible via motor imagery, and when controlling for the possibility of perceptual learning. Importantly, this experiment was completed across several days as this is critical for demonstrating a stable learning effect [179]. The second experiment asks a more subtle question related to what information is derived from motor imagery — that is, if imagery does involve a simulation of a movement, does this simulation produce error signals that can then provide the basis for learning? Finally, the third experiment deploys the same task as the second experiment, but with the addition of simultaneous neurophysiological measurement (electroencephalography; EEG) to allow for the investigation of neural correlates to motor imagery accuracy and determine whether imagery involves a comparative mechanism (that is, comparing intended or expected performance to actual performance — or in the case of imagery, simulated performance) in ways that are similar to overt movement.

Chapter 1 (this introduction) and chapter 5 (General Discussion) was written by Tony Ingram (TI) with suggestion and editorial assistance from Shaun Boe (SB).

Chapter 2 is based on work conducted by TI, Jack Solomon (JS), Dr. David Westwood (DW) and SB. TI conceived the study with assistance from SB and DW. TI was responsible for data collection with supervision from SB. TI and JS were responsible for data processing and statistical analysis and interpretation with assistance from SB. TI wrote the manuscript with assistance from JS, DW, and SB. All authors contributed to revisions prompted by peer review during the publication process.

Chapter 3 is based on work conducted by TI, JS, Austin Hurst (AH), Alexandra Stratas (AS) and SB. TI conceived of the study with assistance from SB. JS and AH refined the experimental task software and pre-processing of error processing. TI and AS were responsible for data collection. TI was responsible for final analysis, statistics, and interpretation with supervision from SB. TI wrote the manuscript with assistance from SB.

Chapter 4 is based on work conducted by TI, AH, AS, Mike Lawrence (ML), and SB. TI conceived of the study with assistance from SB. TI and AS were responsible for data collection. TI, AH and ML were responsible for data processing, including both behavioural and neuroimaging data, figure generation, statistical analysis and interpretation with assistance from SB. TI wrote the manuscript with assistance from SB.

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CHAPTER 2 | MOVEMENT RELATED SENSORY FEEDBACK IS NOT NECESSARY FOR LEARNING TO EXECUTE A MOTOR SKILL

A version of this chapter has been published.

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2.0. ABSTRACT

Sensory feedback has traditionally been considered critical for motor learning. While it has been shown that motor learning can occur in the absence of visual or somatosensory feedback, it is thought that at least one must be present. This assumption contrasts with literature demonstrating that motor imagery (MI) — the mental rehearsal of a movement — is capable of driving motor learning even though the lack of actual execution precludes sensory feedback related to movement. However, studies of MI typically employ simple tasks that do not require improvements in motor execution per se, suggesting that MI might improve task performance primarily through perceptual mechanisms. To avoid this limitation, we designed a novel motor task requiring the repeated execution of unfamiliar kinematic trajectories where learning was assessed through changes in the speed-accuracy function (SAF) across five sessions. General task performance was controlled for by assessing performance on randomly generated trajectories. Groups included physical practice (PP; with and without added visual feedback), MI, and perceptual control (PC), the latter of which only observed the trajectories. All groups performed physically on the final session. Upon the final session, the MI group performed better than the PC group, and better than initial session PP

performance. These results suggest that motor learning occurred in the MI group despite the lack of sensory feedback related to the movement, and that this learning was not simply the result of perceptual learning. Our results question long-standing assumptions about MI based learning and the necessity of feedback in motor learning generally.

2.1. INTRODUCTION

Voluntary movement involves several overlapping and interdependent processes, beginning with the perception of relevant information, goal selection, motor planning, and finally execution [1]. When motor performance improves over time, learning may occur through changes in any of these processes: one can become more adept at recognizing a relevant cue [2], selecting an appropriate goal [3], creating a more effective plan [4], and executing it accurately [5]. Recent work suggests that motor planning, and not execution, is what fundamentally defines the representation of differing motor memories [6]. This is not to suggest that execution isn't important during motor learning — execution gives rise to the sensory feedback that provides a means of assessing the success of a given plan, providing a basis for improving future performance [7–9]. In fact, it is traditionally assumed that at least one modality of sensory feedback must be present for motor learning to occur, namely visual or somatosensory feedback [10,11]. However, there exists considerable literature demonstrating that motor skill acquisition is possible via motor imagery (MI), the mental rehearsal of a motor task [12], even when participants have no prior exposure to the task [13]. This presents something of a paradox: motor learning requires feedback arising from overt execution — yet remains possible during MI, which lacks execution and therefore does not provide sensory feedback related to the movement.

A possible explanation for these findings is that MI gives rise to improved motor performance via changes in perceptual or central mechanisms rather than improvements in motor execution per se [14]. Here we consider perceptual mechanisms broadly, including those involved in recognizing a stimulus and building its representation, and to central mechanisms as those that include such steps as goal selection, sequencing, and stimulus-response mapping [1]. Assessing whether MI based skill acquisition is due to perceptual or central mechanisms as opposed to improvements in motor execution requires careful consideration of the experimental tasks used in MI studies. Like the broader motor control and learning literature [15], MI studies have traditionally employed simple laboratory tasks such as target-directed reaching or keyboard sequence tasks [12–14,16]. In such simple tasks, it is possible to realize performance gains via improvements in perceptual mechanisms (e.g., improved recognition and localization of the target) or central mechanisms (e.g., mapping stimuli to responses) rather than motor mechanisms per se (e.g., improved execution of a movement) [5]. For example, in the case of a sequence keying task, perceiving stimulus "4" cues the goal "press key 4". How the action is subsequently performed — the motor plan — is of little relevance [17], and there is little room for improvement for most individuals. Improved performance is driven by learning the sequence: anticipating, identifying and reacting to stimuli more quickly with a familiar movement, rather than changes in the movement itself [5]. Instead, a more complex task might impose constraints such that "touch location 'x'" requires first reaching around an obstacle ("touch location 'x' like this"). Such a task is inherently more difficult and requires learning a more involved motor plan that includes a specific kinematic path to optimize [4,18]. It may be the case that performance improvements realized through MI are limited to tasks in which perceptual or central mechanisms of learning predominate [1]. In this case, the fact that performance improvements can occur via MI despite the absence of execution and sensory feedback cannot be taken as evidence that motor learning per se can proceed without sensory feedback.

We therefore sought to determine if MI is capable of driving improvements in the ability to execute a novel motor pattern. We designed a task to challenge participants' ability to reproduce a novel movement trajectory using a touchscreen interface. Participants performed the task for five sessions to determine whether performance improvements were retained between sessions [19]. On each trial participants were shown a visual trajectory traced with a white cursor on a black screen, which they were asked to reproduce as accurately as possible, including the speed at which it was animated during presentation (Figure 2.1 A). In addition to pattern trials (i.e., a repeating trajectory representing the movement pattern to be learned), participants also reproduced randomly generated trajectories of similar kinematic complexity (random trials; see methods) to control for general task performance independent of the specific pattern to be learned. Performance was thus assessed for trained and un-trained stimuli in order to determine whether MI led to specific versus general improvements in motor skill. Two physical practice groups were included: one for which only somatosensory and visual feedback of their arm movement was available (physical practice; PP), and another group who additionally received a visual display of their performance upon task completion (physical practice with additional feedback; PPFB). Participants assigned to the MI based practice group (MI) were asked to reproduce the trajectories mentally with kinaesthetic imagery from the first-person perspective [20,21], rather than physically, for the first four sessions until the fifth and final session where they performed as per the PP group without feedback. As participants may improve performance simply through repeated observation of the pattern trajectory [22], a perceptual control condition (PC; see methods for task details) was included where training required attending to the stimulus without responding physically or mentally for the first four days. PC participants observed the same stimuli (random and pattern trials) as all other groups. To ensure that participants paid attention to the stimuli, on completion of each trial they were prompted to enter (by selecting a number from one to five on the touch screen) how many times the cursor changed in a particular direction (i.e. participants were asked "how many times did the dot bounce [direction]?" where [direction] was randomly either left, right, up or down). By including a perceptual observation group, we sought to determine if improvements resulting from MI based practice exceeded what could be attributed to perceptual learning.

We hypothesized that learning would be greatest in the PPFB group, decreased in magnitude for the PP group, and lowest in the MI and PC groups. Given the assertion that performance improvement via MI may be driven by perceptual or central learning mechanisms rather than motor learning, we hypothesized that the MI and PC groups would perform equally by the end of the experiment.

2.2. METHODS

2.2.1. Participants

The Dalhousie University Research Ethics Board granted approval (#2016-3928). Sixty-one participants were recruited with one excluded due to excessive muscle activity during MI (see Electromyography below). As indicated above, participants performed the task in one of four different conditions, with 15 participants pseudo randomized to each. Given that this study utilized a novel experimental paradigm for which no published effect sizes exist, we determined our sample size via power analysis for an expected effect size of learning to be a moderate Cohen's $d = .5$ (or $f = 0.25$) [23]. We performed the power analysis using G*Power 3.1 to determine the number of participants required to detect a moderate effect size with statistical power (1 - beta) of .95, alpha of .05, and assuming we performed a classical statistical analysis of a repeated measures analysis of variance with a within-between interaction (nonsphericity correction epsilon of 1.0), at five measurement times (day one to five, assuming a correlation among repeated measures of .5). All participants provided written, informed consent and were oriented to the experimental task by the investigator. Participants were aged 23.75 ± 5.34 (mean ± SD) years, 42 identified as female, and 3 were left handed and 1 ambidextrous according to the Edinburgh Handedness Inventory [24].

2.2.2. Task Description

Participants were asked to perform a novel behavioural task using custom software developed in the Python (version 2.7) programming language (https://github.com/LBRF/TraceLab). Participants sat at a 24" touchscreen (Planar PCT2485; 1920 x 1080 resolution) enclosed within a black box to reduce distractions and ensure screen illumination was constant across sessions and participants (Figure 2.1 A). Participants completed the task using their dominant hand. Sessions were scheduled such that each occurred at least one day apart, but no more than three weeks from first to last, for each participant. At the end of the experiment, the average difference (in days) between the first and final sessions was 6.33 (standard deviation = 2.59) and an analysis of variance revealed no significant difference between groups ($p = .27$).

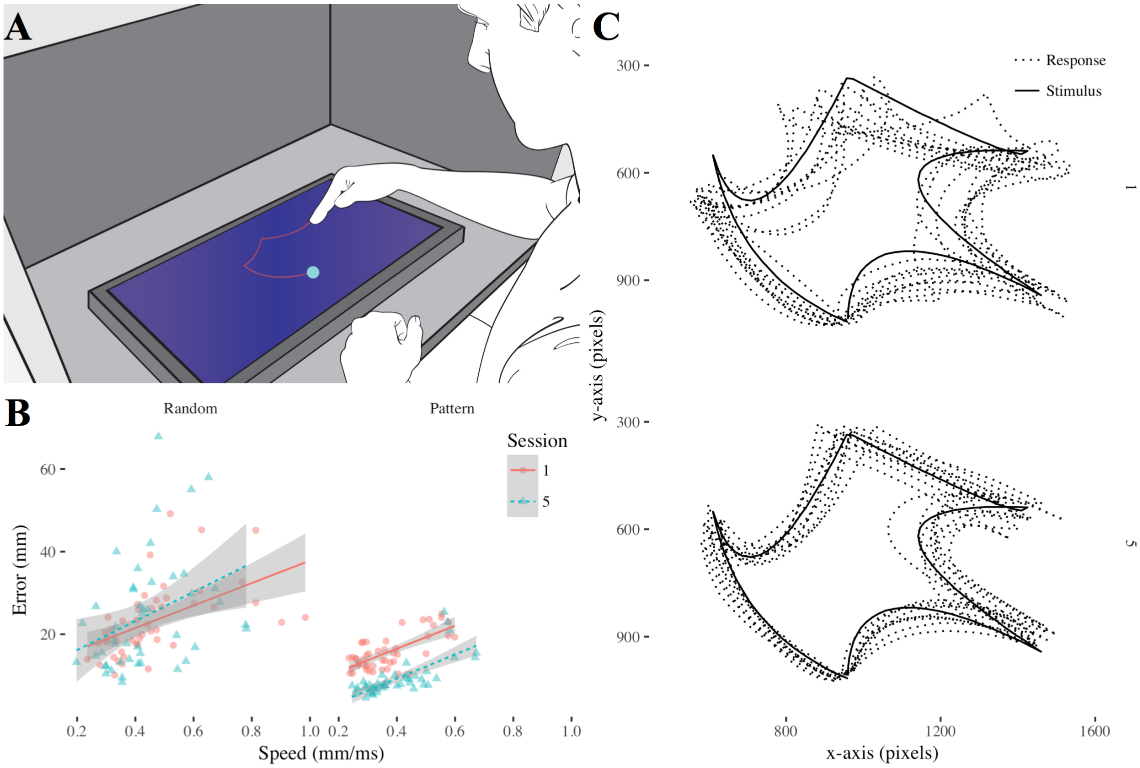

Figure 2.1. A. Example trial illustrating a typical trajectory. Note that the real-time tracing shown above is for illustrative purposes only and no such feedback was provided to any group. The PPFB group received feedback of their performance after each trial ended. B. Representative participant's SAF from session 1 to 5 illustrated by plotting error as a function of speed for the random (left) and pattern (right) trials. A regression line with 95% confidence interval shading is plotted to aid interpretation. Note the decrease in error at all speeds — denoted by a rightward shift in the SAF — from the first to final sessions for the pattern trials. This decrease in error is not evident in the random trials. C. The same representative participants first (upper panel) and final (lower panel) session tracings (responses), overlaid upon the target pattern (stimulus) as recorded from the touchscreen. Note the decrease in kinematic error and variability.

Trials began with the participant tapping the screen to trigger a white dot that travelled from a starting location on the midpoint of the lower half of the screen. All trajectories made curved paths between four additional points and ended at the starting point to create a five-segment trajectory that animated clockwise from point to point. Trials consisted of either randomly generated trajectories or a pattern trajectory that repeated (i.e. the motor skill to be learned) with similar characteristics as those that were randomly generated (i.e., path length, complexity and curve characteristics; described below).

Segment end points were connected with a constrained minimum linear acuteness to ensure that vertices were visible to the participant. Points were pseudo randomly generated such that at least one was present in each quadrant of the screen, with inner and outer margins set to ensure points were not generated too closely to each other, or to the outer edge of the screen. Curves were animated by generating Bezier curves with randomly generated control points that determined curve peak magnitude, shift and shear. Constraints on control points were set to ensure characteristics varied within a reasonable window as determined through pilot testing. Trajectory path length was allowed to vary so that all other features could vary flexibly between randomly generated trajectories while minimizing computational load. Varying trajectory speeds were achieved by pseudo randomizing five animation times (500, 1000, 1500, 2000, and 2500 ms) such that each had equal exposure. All settings and constraints described here were determined reasonable via pilot testing, and exact numbers used during the experiment are set as defaults on the version hosted at the link provided above.

Within a single session, a participant performed 50 random and 50 pattern trajectories, pseudo randomized within five blocks (20 trials per block: 10 random, 10 pattern) such that exposure to each condition (i.e. pattern or random) was even throughout the experiment. Within each block, participants were exposed to each of the five animation times pseudo randomized to occur twice for each condition.

Immediately upon completion of a trajectory animation, a red circle appeared at the end location. Participants were instructed to touch this circle to begin reproducing the trajectory they had just observed. Successful contact with the red circle turned the circle green, indicating that their response was being recorded. Importantly, participants were asked to match both the shape and speed of the trajectory observed. That is, participant response speed was not constrained (i.e., rejected if too slow or too fast) but instead was allowed to vary naturally, allowing for a more continuous sampling of movement speeds (see Speed Accuracy Function below for analysis details). Finally, the green circle disappeared upon the participants return to the end location thereby marking the end of the response and thus the trial. Movement time (MT) was operationalized as the time between the beginning and end of a trial — that is, how long the green circle was on the screen. Participants in the PPFB group received additional visual feedback, immediately following the end of each trial, in the form of a tracing of their response (in blue) overlaid upon a tracing of the trajectory they were supposed to recreate (in white). Sensory feedback can provide either knowledge of performance or knowledge of results, though the latter is typically associated with visual feedback rather than somatosensory; one can see and feel themselves shooting a basketball but cannot feel the result at the net. As the PP and MI groups did not receive knowledge of results in this experiment, we thought it would be useful to include the PPFB group with added visual results feedback.

MI participants performed the task similarly with the only difference being that when placing their index finger on the green circle to initiate their response, their finger remained in place while they performed imagery of the movement. MI participants were asked to simply lift their finger from the screen upon completion of each imagined trial. This approach allowed for the quantification of imagined MT, which was then used to perform mental chronometry, providing evidence that MI participants performed the task as instructed. Mental chronometry was performed by assessing whether a relationship existed between stimulus MT and imagined MT, and to compare imagined MT to actual (physically executed) MT.

Given that PC participants performed a considerably different task as described in the introduction, MT was collected but not used in analysis. For PC participants, MT represented the time between the participant beginning to select their answer, and ending when they entered “submit”.

2.2.3. Electromyography

To ensure participants assigned to the MI group were not physically performing the task (i.e., engaging in MI with minimal muscular activation), electromyography (EMG) was recorded to allow for monitoring (and subsequent quantification) of muscle activity during MI sessions. EMG was recorded using self-adhering Ag/AgCl electrodes (3 x 3 cm; Kendall-LTP, Chicopee, MA), affixed to the skin overlying the anterior, lateral and posterior shoulder muscles (deltoids) of the arm performing the task. The raw EMG signal was bandpass filtered (0-333 Hz) and sampled at 1000 Hz (1902 Amplifier and Power 1401, Cambridge Electronic Design, Cambridge, UK) and stored for offline analysis. If a participant displayed muscle activity greater than two standard deviations of their resting baseline for more than 20% of their MI trials, they were excluded from the analysis. This occurred for only one participant.

2.2.4. Pattern Trial Trajectories

Participants were exposed to one of five possible pattern trial trajectories to induce a practice (and subsequently learning) effect. These pattern trajectories were selected to ensure their characteristics were as similar as possible to random trajectories: each consisted of five segments with the same constraints. To account for features that vary for random trajectories (i.e. path length and the two measures of complexity described below) pattern trajectories were selected to fall narrowly within half a standard deviation of their median value. This was achieved by generating 10,000 random trajectories with the same constraints as those to be used in the random condition for the experiment and subsequently measuring path length and complexity. These 10,000 trajectories were then narrowed down to those within half a standard deviation of each measure. The remaining trajectories were randomly selected and visually inspected to avoid problematic features as determined through pilot testing: we avoided 1. trajectories that came too close to the end position part way though the animation to avoid participants accidentally ending a trial early, 2. trajectories that included difficult to identify vertices (despite the minimum linear acuteness constraint) and 3. trajectories whose curves were not evenly distributed between quadrants to avoid bias toward a particular area of the screen to avoid participants changing their positioning over the course of the experiment.

2.2.5. Complexity Measures

Experiments in motor control and learning often manipulate task complexity by altering task and environmental constraints (juggling two versus three balls; juggling on a stable versus unstable surface). But how does one characterize task complexity when such constraints are fixed? One method would be to characterize kinematic complexity. We used two complimentary measures: 1. total absolute curvature, and 2. approximate entropy. Total absolute curvature is a measure of the magnitude of curvature over the course of a trajectory. Curvature has been used to characterize movement complexity in previous work [4], where it is thought that — when controlling for speed — more curved movements involve greater and more frequent changes in muscle activity [25,26]. As the trajectories in the current study involved discontinuities at segment end points (vertices), total absolute curvature was approximated by taking the sum of point-by-point turning angle. Approximate entropy is a measure of the predictability of a sequence [27]. Approximate entropy is useful for characterizing biological motion even in short data sets when used appropriately [28]. Together, these two measures allow for characterization of kinematic complexity operationalized as the magnitude (total absolute curvature) and irregularity (approximate entropy) of a trajectory's curvature. Complexity was measured for stimulus trajectories — not participant responses — as it was used mainly to ensure the chosen pattern trajectories were adequately similar to randomly generated trajectories (see 'Pattern Trial Trajectories' above).

2.2.6. Response Error

Participant response error was measured as the ordered point-by-point Euclidean distance in millimeters (mm) between stimulus and response trajectories. When stimulus and response lengths (that is, the number of samples) were different, the longer sequence was down sampled to the shorter to allow the point by point error calculation. As each sample was collected with a timestamp, calculations of speed were not affected by down sampling. Using this method of error measurement, it is possible that two different responses result in a similar error magnitude despite one having a more accurate “shape”. To elaborate, if two participants were tasked to trace the same triangle, and one traced a similarly sized rectangle, while the other traced a triangle that was too small, it is possible that the small triangle would result in error equal to the rectangle despite being the “correct” shape. To ensure error represented participant’s ability to reproduce the shape of the trajectory — independent of translation, rotation and scale — participant responses were subject to Procrustes transformation using the stimulus trajectory as a template [29]. Procrustes transformation has been used in the analysis of human movement in previous literature [30]. Further, we ensured participants were not penalized for natural human variation in movement speed. That is, it is reasonable that participants would move faster on straight or minimally curved paths while slowing down on sharp turns. We wished to allow for such variability in movement speed within a trial. Stimuli were animated and therefore sampled at a constant speed. Dynamic time warping was used to optimally transform participant response trajectories onto stimulus trajectories [31], allowing for error measures that are insensitive to local compression or stretches due to variability in timing. Procrustes and dynamic time warping transformed participant response trajectories were finally compared to the stimulus trajectory by calculating the distance between associated points in each time series. Response error for a given trial was calculated as the mean of this point by point distance (Figure 2.1 B illustrates mean error per trial as a function of speed). Response speed of a trial was calculated as the total path length divided by the movement time (as described in ‘Response’ above).

2.2.7. Speed Accuracy Function

Bayesian multi-level modelling was adopted to perform statistical inference on the magnitude (Cohen's d effect sizes; ES) and corresponding uncertainty (95% Highest Posterior Density Interval; 95% HPDI) for each group's performance by block over the course of the experiment, each groups learning from the first to last blocks of the experiment, and between group differences in learning [32]. Bayesian statistical inference was used to analyze the present work for the following reasons: 1. Bayesian modelling allows for convenient modelling of how the experimental manipulations affect a parameter of interest — in this case, the shift of the SAF function — rather than being restricted to interpreting the slope or intercept as per linear regression, 2. once the size and uncertainty (posterior density) of parameters of interest are estimated, one can perform inference on any comparison of interest without additional statistical tests, since Bayesian inference does not fall prey to the problem of multiple comparisons, which is desirable given that our design involves numerous groups, conditions and sessions, 3. Bayesian modelling easily handles missing data, which is highly beneficial given that the MI and control groups do not have any speed or error data for the first four days of the experiment. For those less familiar with Bayesian statistics we suggest the technically incorrect but useful conceptualization of a 95% HPDI as analogous to a classical 95% confidence interval, and highly recommend the recent review by Kruschke and Liddell for a well written and intuitive explanation [32].

Given that extensive previous research indicates that SAF's are typically sigmoid functions where error increases as a function of movement speed [33,34], we modelled data using the generalized logistic equation [35]:

$$error = B + \frac{A - B}{1 + e^{-C\,(speed\,-\,D)}} \tag{1}$$

where *A* is the upper asymptote of error (in units of mm for the present experiment), B is the lower asymptote, *C* is the maximum slope, and *D* is the speed (in units of mm/ms for the present experiment) at maximum slope. Improved performance is represented as a rightward shift in the function over time, modeled by a larger *D* term.

It should be noted that although observed data may give the impression that the function changes shape over time (e.g. lowering *A*), or might take a logarithmic shape rather than logistic, this is most likely an artefact of limited sampling across possible speeds. That is, if participants were required to perform the skill at ever higher speeds one should eventually observe the same upper asymptote of error, and at ever lower speeds and therefore without a time constraint, one could theoretically perform the movement perfectly. Therefore, the only term in the model allowed to vary by experimental manipulation (e.g. time, random versus pattern trajectories, and group) was D.

Participant speed and error data were scaled from 0 to 1 to allow for intuitive, standardized priors. The upper asymptote parameter *A* was allowed to vary globally (but not between experimental manipulations) with a prior centered at 1 (the highest observed error). The lower asymptote *B* was removed from the equation, effectively constraining it to zero (theoretically perfect performance given an unlimited movement time). The maximum slope parameter *C* was allowed to vary globally with a prior centered 1 (given that the speed and error axes both ranged 0 to 1). Finally, the global intercept parameter

D_0 had a prior centered at 0.5 given the scaling of the data, and all other effects in the linear model of D were modelled as deflections from D_0 centering priors at zero. Uninformative but regularizing (non-uniform) priors were used throughout. Therefore, the final model was:

$$
\begin{aligned}
error_i &\sim N(\mu_i, \sigma) \\
\mu_i &= \frac{A_0}{1 + e^{-C_0\,(speed_i - D_i)}} \\
D_i &= D_0 + D_{group[i]} * D_{session[i]} * D_{block[i]} * D_{condition[i]} + D_{participant[i]} \\
A_0 &\sim N(1, 1) \\
C_0 &\sim N(1, 1) \\
D_0 &\sim N(.5, 1) \\
D_{effects} &\sim N(0, 1) \\
D_{participant} &\sim N(0, \sigma_{participant}) \\
\sigma_{participant} &\sim \mathrm{HalfCauchy}(0, 2) \\
\sigma &\sim \mathrm{HalfCauchy}(0, 2)
\end{aligned}
\tag{2}
$$

All available error and speed data, from each trial of each participant, were fit to the model using Hamiltonian Monte Carlo sampling as implemented in Rstan. To aid in interpretation, posterior probability densities for SAFs were simulated using the generative model derived via Bayesian model fitting and plotted in Figure 2.2. The posterior was then sampled to obtain the SAF shift (term D_i) for each group, session and condition to produce plots, effect sizes and their respective HPDI for interpretation.

2.2.9. Performance and Learning

Performance was operationalized as the SAF shift during pattern trials after subtracting the SAF shift during random trials (displayed in Figure 2.3); that is, the degree to which participants were better at the repeated pattern trajectory compared to unrepeated random trajectories. Learning was operationalized as the difference in performance between blocks and most importantly as the difference between the first and final blocks of the experiment. Learning is best operationalized as a between session difference in performance, as within session performance can differ for many reasons (attention, fatigue, etc.) and do not reflect a "relatively permanent" change in performance [19]. This poses a challenge for researchers studying motor learning of a novel skill via MI — by assessing performance at the beginning of the experiment, subsequent MI practice is no longer that of a novel skill; and inversely, if one does not assess physical performance prior to MI, baseline performance is not available — as is the case with the present experiment. Fortunately, in our case the initial session of the PP group affords a truly naïve baseline: a performance measurement unaffected by prior exposure to the physical task or any other training method such as MI, and for which task conditions are identical (no additional feedback) to the final session of the MI and PC groups. Therefore, learning was assessed in the MI and PC groups by comparing their final block (block 25) performance with the initial block (block 1) performance of the PP group. PPFB was compared to its own initial performance as it better reflected the initial task conditions (additional feedback).

Mental chronometry was also analyzed using Bayesian statistics but with a simple linear regression model predicting imagined MT from stimulus MT. The perceptual control task was analyzed by first calculating an effect size for the difference in their accuracy from random chance to ensure they were attending to and performing the task as instructed, and then using regression models to assess whether performance changed across the four training sessions in pattern or random trials.

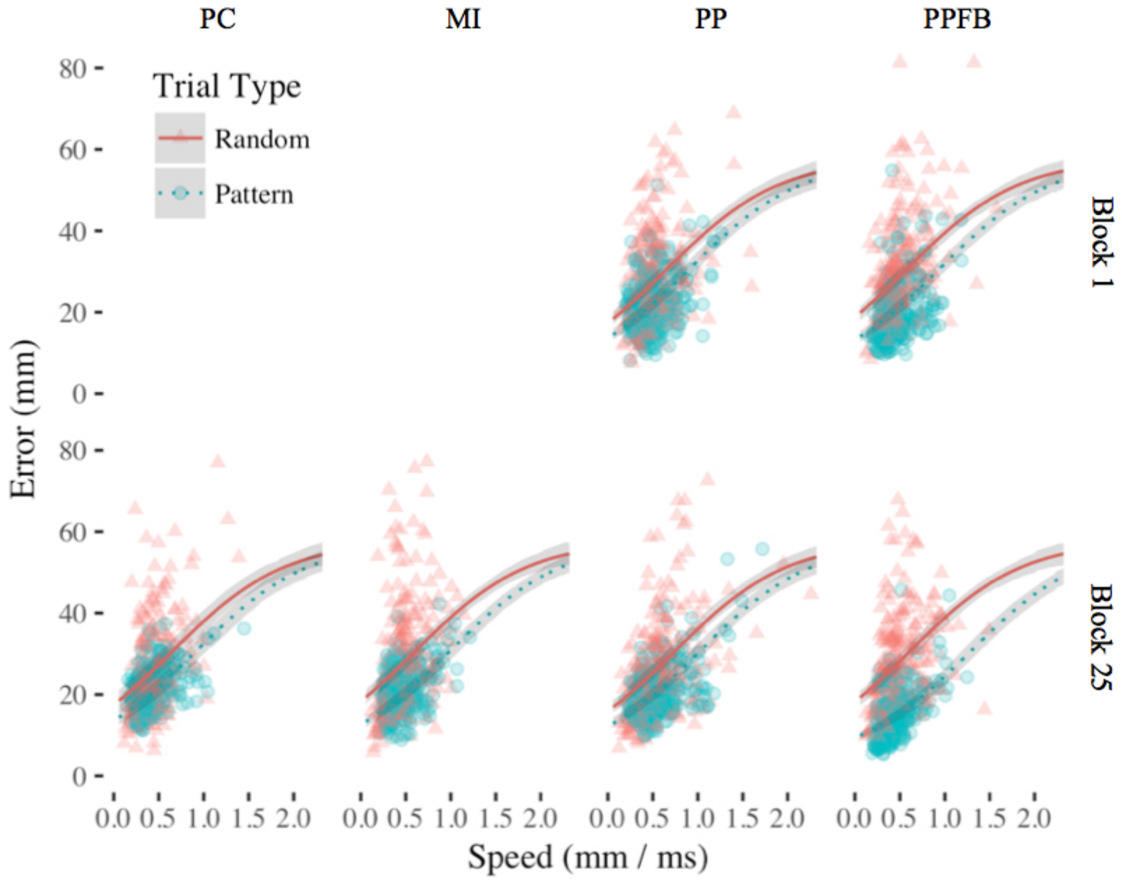

Figure 2.2. Fitted SAFs from beginning (block 1) to end (block 25) of experiment for each group. Lines illustrate the mean error with shaded 95% HPDI) of an average participant. No data was available for first 20 blocks of PC and MI. The larger distance between random and repeated trials in the final block compared to the first is particularly clear in the PPFB group. Note the higher density of trials performed at lower speeds, which is indicative of participants tendency to approach a comfortable speed when allowed to self-pace their responses, particularly near the end of the experiment. This illustrates the importance of assessing motor performance through modeling the SAF. Bayesian modeling handles this variability in sampling; as less data is collected at higher speeds, estimates are less certain and the HPDI becomes wider.

2.3. RESULTS

We confirmed MI participants conformed with the instructions to imagine the required movements at the correct speeds by comparing their imagined MT to the animation MT (i.e., mental chronometry). MI participants modulated their imagined MT according to the stimulus MT during imagery sessions (i.e., sessions one to four; modeling participant MT as a function of stimulus MT; intercept: 1.10, 95% HPDI: 1.05 to 1.15; positive slope: 0.82, 95% HPDI: .78 to .85). While MI participants were generally slower (longer MT) than PP participants during imagery sessions (MI mean MT (seconds): 2.33, SD: 1.13; PP mean MT: 1.92, SD: 0.78), this difference became negligible on the fifth session when MI participants performed the task physically (MI mean MT: 1.98, SD: 0.75; PP mean MT: 1.84, SD: 0.70).

Next, we sought to ensure that the PC group performed the perceptual observation task during the initial four sessions as asked, and whether this led to learning of the movement patterns they observed. Participants in the control condition demonstrated generally low error on the perceptual observation control task relative to chance (mean absolute error: 0.78, SD: 0.75; simulated random responses mean: 1.41, SD: 1.04; ES of difference in means: 0.68, 95% HPDI: 0.15 to 1.13), suggesting that they were indeed paying attention to the perceptual stimuli. Furthermore, PC participants demonstrated slightly better performance on pattern compared to random trials over time (a negative mean slope of absolute error across blocks was found on pattern trials: -0.011, for which the 95% HPDI only slightly overlaps with zero: -0.017 to -0.004; but this was not the case with random trials which were centered close to zero: -0.0002, 95% HPDI: -0.005 to

0.004), providing a baseline estimate of the degree of perceptual learning that could be expected through repeated visual exposure to the pattern trial stimuli.

We then interpreted the main experimental findings by assessing the results of the model fit. At all trajectory speeds, participants in all groups were more accurate for pattern compared to random trials (Figure 2.2). This finding was apparent by the end of the first block of the experiment, demonstrating rapid learning of the pattern after only 10 trials (Figure 2.2, block 1). Throughout the experiment, performance on random trials was static while performance on pattern trials improved, leading to a larger rightward shift in the SAF as training progressed (Figure 2.2, block 25; the fifth block of the fifth session). Given that initial (session one) performance is not available for MI and PC groups, we inferred whether each groups baseline performance was similar, by assessing mean performance on random trajectories only (as opposed to the difference between pattern and random SAF's) for the first block whereby each group performed physically. Random trajectory performance is therefore the position (rather than the shift) of the SAF (speed at maximum slope in units of mm/ms), and will be termed "random performance" to avoid confusion. Random performance for all groups was similar at baseline with highly overlapping HPDIs (mean random performance of PC group: .28, HPDI: .24 to .34; MI group: .24, HPDI: .20 to .30; PP group: .29, HPDI: .24 to .33; PPFB group: .23, HPDI: .18 to .28). Even after four days of training, PP and PPFB groups improved their random performance only slightly (session five block one mean random performance of PP group: .34, HPDI: .29 to .39; PPFB group: .29, HPDI: .24 to .35) and were not significantly different from the PC and MI groups (highly overlapping HPDIs). This similarity in random performance provides evidence that baseline task performance was comparable between all groups.

Again, using simulations from the generative model, each group's performance — their SAF shift on pattern trials minus the SAF shift on random trials — was plotted for all blocks in Figure 2.3. We found a very large effect of learning from the first to final block (block 25; Figure 2.3) in the PPFB group (ES: 3.31, 95% HPDI: 1.75 to 5.17; Figure 2.3). The PP (without feedback) group demonstrated a small effect of learning from the first to final block of trials, but a large portion of the interval overlapped with zero (ES: 0.35, 95% HPDI: -0.56 to 1.30; Figure 2.3). Taken together, the results from the two PP groups suggest that learning is greatly enhanced when added visual feedback is available.

The MI group demonstrated a large effect of learning from the first to final blocks (ES: 1.19, 95% HPDI: 0.19 to 2.37; Figure 2.3), and the PC group demonstrated a negligible effect of learning whose interval overlapped considerably with zero (ES: 0.13, 95% HPDI: -0.78 to 1.07; Figure 2.3). These results indicate motor learning did not occur in the PC group despite the control task results reported above showing that this group learned to recognize the repeated pattern better over the course of the experiment.

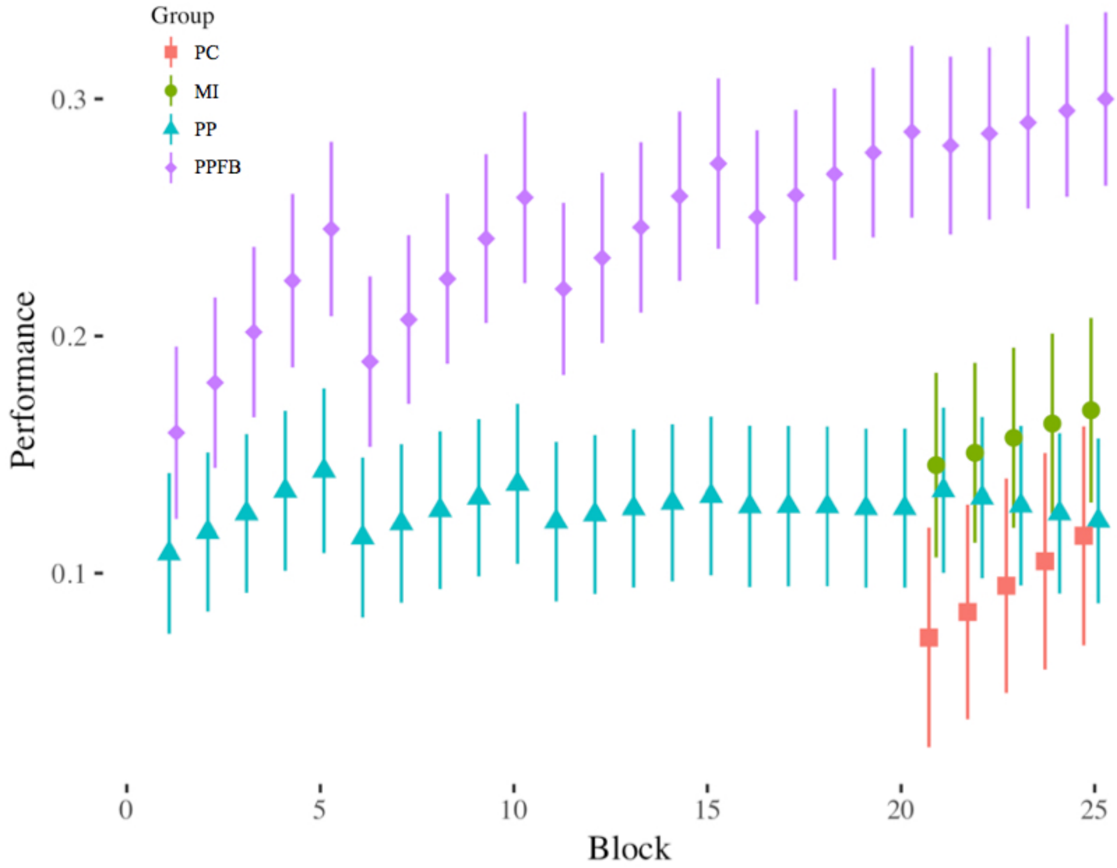

Figure 2.3. Learning across experimental blocks for each group as per the fitted model. Performance was operationalized as the difference between pattern and random SAF shifts, and is presented as mean ± SD. Learning can be observed as increases in performance over time. Estimates are not presented for sessions one to four in MI and PC groups given that no physical performance data was collected for these blocks. When compared to initial block performance in the PP group, MI clearly outperforms the PC group on physical testing during the final session.

2.4. DISCUSSION

Overall, the finding of a greater effect of learning for the MI group compared to the PC group leads us to question long-standing assumptions about MI based learning and the necessity of feedback in motor learning generally. Specifically, our results indicate that engaging in MI based training improved motor execution of a novel kinematic pattern, rather than improving performance due to perceptual learning. This conclusion is underscored by the relative absence of learning in the PC group, which suggests that motor learning via MI cannot be attributed to simply improved recognition of the stimulus. Our hypothesis is partly supported, in that learning appears to have been greatest in the PPFB group, then MI, then PP, and then PC. Overall these results suggest that when using an appropriate experimental design, MI appears to be capable of driving motor learning of a complex motor pattern, improving one's ability to execute the plan despite lacking prior physical experience.

That PP without added visual feedback failed to demonstrate a robust learning effect over the course of the experiment might appear surprising. One might expect at least some learning to occur due to use-dependent learning, where repetition of a movement direction biases it for future movements [36,37]. However, use-dependent learning is typically demonstrated using simple tasks, and complex trajectories involve a variety of directions which may preclude a biasing in any particular direction. Still, previous work has shown that participants exhibit motor learning even when both visual and somatosensory feedback is disrupted [38]. However, the nature of feedback is of critical importance: in the study cited above, participants had their arm sensation disrupted via vibration and view of their arm occluded (disrupted performance feedback) but were still able to view the position of a cursor representing their performance (intact results feedback). When a participant can see the results of their actions they are able to improve their performance and learning can occur, even if their sensation of that action is disrupted. However, when results feedback is restricted — like shooting a basketball and closing one's eyes immediately after the ball leaves the hands — there is no basis to determine what corrective movements will adjust the plan to achieve the goal more effectively. That is, there is no error signal related to the goal. We believe our findings demonstrate that a lack of results feedback may be disruptive to between-session learning when training a complex movement skill via PP. That said, it should be noted that the PP group did slightly improve on random trajectory performance as stated above, and that this may underrepresent the true effect of learning in the PP group (indeed, this would be the case for the PPFB group as well). Though it may be less certain than for other groups, the results suggest that it is more likely the PP group learned. Given the lack of improvement in the PC group that will be discussed below, the larger learning effect observed in the PPFB group is likely driven by the provision of additional error information, rather than extra stimulus exposure afforded by the presentation of feedback.

Despite a lack of results feedback throughout the experiment we observed a significant learning effect in the MI group. Although it might be tempting to assert that these improvements are simply the result of perceptual learning of the movement pattern over repeated exposure, the results show that learning in the MI group was significantly higher than that observed in the PC group (ES for difference between MI and PC: 0.82, 95% HPDI: 0.28 to 1.51). These results support the notion that motor learning can occur in the absence of any sensory feedback. This differs importantly from learning that may occur at other stages on the path from perception to action, such as perceptual learning, goal selection or stimulus-to-response mapping. Our results do not preclude MI from being capable of supporting learning through these earlier stages; indeed, evidence exists suggesting that it does [14]. The significance of the present result is that MI appears to also drive learning at a later stage of processing: developing and improving upon a motor plan

— and therefore execution — even in the absence of results feedback. While previous work indicates that motor learning can occur without outcome information through use-dependent learning as discussed above, this is not possible during MI as execution never occurs. That the absence of results feedback did not disrupt motor learning via MI suggests that perhaps alternative learning mechanisms that do not depend on such feedback are at play. Motor learning via MI may result from a simulation mechanism whereby a forward modeling process determines the likelihood that a motor plan would be successful, thereby providing a basis for improving the plan [39]. Indeed, this notion of MI recruiting the forward model to predict the sensory consequence of imagined movement has recently been demonstrated [40].

Our results are best explained by acknowledging that MI is not simply motor planning without movement, but a fundamentally different process. Evidence for such an assertion exists in both basic and applied research. Neuroimaging research consistently reveals overlapping but different neural circuits associated with MI compared to motor execution [41]. For instance, both MI and overt motor performance activate largely similar frontal and parietal networks [42,43]. However, sensorimotor areas engaged during MI are more associated with motor planning than execution, demonstrating more rostral than caudal contralateral primary motor cortex [44], more ventrocaudal than dorsorostral ipsilateral cerebellar activity [45], more rostral than caudal SMA activity [46], and more caudate nucleus rather than posterior putamen activity in the basal ganglia [46]. Applied studies also appear to demonstrate that MI is different from PP, rather than less effective. Although PP is often shown to be superior to MI alone, a combination of MI and PP tends to result in greater training related gains in performance compared to PP alone, even when controlling for total practice time [47,48]. Theoretically, MI is thought not to simply include motor planning without subsequent execution, but a simulation of movement as well as the sensory feedback likely to result [39]. Some have postulated that motor execution also relies on these simulations to assess feedback for online movement correction (e.g. forward models as per the computational sensorimotor control literature) [49]. However, while feedback is expected during physical execution, it is not during MI — which may further explain our result of negligible learning in the PP group. MI on the other hand may rely solely on simulation of the motor plan — while disengaging mechanisms depending on feedback — and learning occurs by adjusting the plan to correct perceived differences between simulated and desired outcomes.

Limitations of our work center around the nature of both the motor and perceptual control tasks, as well as those inherent in MI research. Human performance of complex tasks can be considerably variable, and in the case of this experiment such variability can be observed clearly in Figures 2.1, 2.2 and 2.3. We attempted to take advantage of this variability, rather than average it out, by using multi-level modelling in our statistical analysis. Another important limitation is the inherent difficulty in mapping behavioral tasks to theoretical cognitive processes: namely whether the motor task truly captured late stage motor processing, or whether the perceptual control task truly captured perceptual learning. It is conceivable that such processes are highly parallel and interdependent, and thus impossible to isolate exclusively. Next, the lack of robust learning observed in the PP group might have simply been due to frustration or boredom on part of the participant given the lack of reward, whereas MI may be more engaging given that it reportedly requires more effort. Indeed, it was an attempt to combat boredom that motivated the PC task design to include a touchscreen response after each trial, which itself could have altered the PC task in such a way as to reduce its comparability to the motor task. However as discussed above, methodological limitations could have also affected the PP group result. Finally, the poor performance of the PC group might have been due to interference via altering the nature of the task, however we feel this would have been reflected in the random performance analysis performed. Overall, given that the nature of MI precludes its accurate measurement — we cannot observe or measure exactly what others are imagining — operationalizing learning and designing carefully controlled experiments will always be a challenge.

In conclusion, our results demonstrate that MI based practice can drive motor learning of a kinematically complex multi-articular motor skill in the absence of feedback. We propose that learning a motor plan during MI may depend on simulation of the motor plan. Future work will require a combination of well-designed neuroimaging and behavioural studies to disentangle the mechanisms driving simulation-based and feedback-based mechanisms involved in motor learning. Our results appear to indicate that feedback-based motor learning (as per the PPFB group) is much more effective than simulation-based motor learning (as per the MI group) alone — determining why this is the case would be a boon to improving applications to neurorehabilitation, vocational and sports training. Further, are these mechanisms complimentary, and if so, are they additive or do they interact to provide multiplicative results? When PP is not possible — as is often the case in neurorehabilitation and injured athletes — how might neurofeedback affect MI based training? Answering these questions and more will require investigators to employ experimental tasks that capture more aspects of motor learning than those traditionally employed.

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CHAPTER 3 | IMAGINED MOVEMENT ACCURACY IS STRONGLY ASSOCIATED WITH DRIVERS OF OVERT MOVEMENT ERROR AND WEAKLY ASSOCIATED WITH IMAGERY VIVIDNESS

3.0. ABSTRACT

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

3.1. INTRODUCTION

Motor imagery and its relationship with overt movement and motor learning remains an active area of debate [1–3]. Interest in motor imagery is driven to a large degree by its potential applications — particularly as a modality to drive motor learning in neurological rehabilitation [4–6]. It is therefore critical to understand the mechanisms of imagery-based motor learning, which is typically investigated by comparing imagery to overt movement. Theories of motor imagery posit varying levels of similarity between imagery and overt movement. The highly influential motor simulation theory claims functional equivalence such that, aside from the absence of movement, motor imagery involves the same computational and neurophysiological processes as overt movement [7,8]. Competing theories propose that motor imagery is largely an abstract cognitive process that does not recruit the motor system [9]. More recently authors propose a middle ground whereby motor imagery shares in some processing involved in overt movement, such as motor planning, but then diverge into an entirely different process when the movement reaches the execution stage [2]. It has also been proposed that motor imagery involves a simulation of movement execution, recruiting parts of the motor system to perform this simulation without executing the movement overtly [1]. Depending on experimental details, behavioural and neuroimaging studies provide limited support for any one of these perspectives. That is, motor imagery and overt movement share activation patterns in some brain regions, but also show differences in others [3,10]. Thus, it remains unclear how imagery may be used to drive motor learning in a way that derives similar benefits as practicing via overt movement.

The variety of results reported in the literature may be explained by the wide range of tasks used. Several potential processes may be differentially recruited depending on the demands of the experimental task. Overt movement is understood as involving several interdependent processes, such as perceptual processing, goal selection, decision making, motor planning, action selection and finally execution [11,12]. Improvements in performance — and over time, learning[13] — can be attributed to changes in any combination of these processes. For instance, one may learn to better recognize patterns that shape task demands [14], create or refine a motor plan [15], or improve the quality of movement execution [16]. Experimental tasks such as serial reaction time (SRT) tasks likely bias the participant to rely on perceptual or cognitive rather than motor processes [16–18]. Few motor imagery studies utilize tasks that challenge motor execution and assess performance changes via the speed-accuracy function [19,20], which is considered the preferred method of assessing the quality of motor execution [16]. We propose that at least part of imagery's apparent reliance on perceptual and cognitive functioning is due to the use of experimental tasks that challenge those functions and do not adequately challenge movement execution.

We recently demonstrated that motor imagery is indeed effective for learning to execute a novel motor skill [19]. This was achieved using an experimental touchscreen task that involved complex, multi-articular movements that were either randomly generated or repeated, measuring performance via changes in the speed-accuracy function. Importantly, the results could not be explained by perceptual learning alone. Given that motor imagery lacks sensory feedback, the existence of motor learning via imagery appears paradoxical. Sensory feedback is regarded as necessary for motor learning [21], as either visual or somatosensory information provides error signals that can be used to make adjustments both during performance and in subsequent attempts [22,23]. However, given that motor imagery may involve a simulation of the executed movement, it is possible that participants have access to the quality of this simulation — consciously or unconsciously — and therefore are able to make refinements to a motor plan based only on a comparison between the intended outcome and the predicted outcome [24]. Indeed, it is well established that sensorimotor control involves forward models that predict the sensory consequences of an action as it unfolds, which allows for corrections earlier than can be explained by sensory feedback alone [25,26]. It has been demonstrated recently that motor imagery also involves the use of forward models to predict the sensory consequences of an imagined movement [27]. Thus, during repeated motor imagery-based practice performance improvements may be driven by comparisons between predicted and intended outcomes of the imagined movement. Alternatively, the motor-cognitive model of imagery supposes that while overt action is able to rely on unconscious and automatic processes such as forward models, motor imagery is unable to utilize these processes [2]. Instead, motor imagery utilizes executive processes to consciously elaborate upon abstract representations of the movement. More complex tasks require greater executive resources to form a representation and therefore give rise to increased movement times compared to overt action. One can interpret this as implying that rather than imagery involving the processing of predicted error, imagery is instead an exercise in creating an abstract image of a movement and refining it. That is, as participants are repeatedly exposed to the movement to be imagined, they simply refine their representation to make it more vivid, rather than simulate its execution and assess its accuracy. It therefore remains an open question whether imagery-based motor learning is the product of processing simulation error or the product of refining the vividness of an error-agnostic representation.

To answer this question, we utilized a previously established experimental task [19] that involves participants replicating a kinematically complex movement pattern at varying speeds on a touchscreen either overtly (overt group) or through motor imagery (imagery group). Varying speeds allowed for the assessment of the speed-accuracy function to investigate the quality of movement execution. The task includes both a repeated pattern assigned to the participant (repeated condition) as the task to be practiced, as well as randomly generated patterns (random condition) that are novel throughout the experiment. While it can be argued that no movement is completely novel as it may be comprised of familiar movement components (e.g., primitives) [28–30], more complex movements can be sufficiently novel combinations of familiar patterns. Movement pattern complexity varied in the random condition as well as across participants with respect to the pattern they were assigned. Importantly, after every trial we asked participants in each group (both overt and imagery) to self-report how accurate they believe their performance was. At the end of each block for the imagery group only, we asked participants to rate how vivid their imagery had been in the preceding block of trials. Given that the overt group will have overtly performed the movement and are therefore afforded sensory feedback, their self-reported accuracy should have a strong relationship with their performance as measured by the speed-accuracy function. However, if motor imagery does not involve error processing and instead involves only the elaboration of a representation, participants self-reported accuracy during imagery may be a function of the number of trials for which they have formed the image, and may be related to their vividness ratings, but will not have a strong relationship with the error you would expect given the speed and complexity of the task. That is, in the imagery group compared to the overt group, the movement pattern will not be sensitive to known drivers of performance (e.g., speed) and self-reported accuracy will have a weaker relationship with performance as measured by the speed-accuracy function, and variability will instead be best explained by their vividness ratings. Given previous findings that motor imagery involves the use of forward models [27] and that imagery participants appear to be able to report their accuracy [24], we hypothesized that imagery participants self-reported accuracy will indeed have a strong relationship with their expected error. We also tested whether self-reported accuracy changes across trials in the repeated condition compared to the random condition to investigate whether error processing during imagery evolves similarly to overt practice — that is, we hypothesized that imagery is indeed capable of forming novel motor representations in the absence of previous overt experience and updating the representation in an experience-dependent fashion similar to the overt group. Finally, we analyzed whether movement complexity had a differential effect on movement time between groups. Importantly, our experimental task involved variation in the kinematic complexity of the movement pattern rather than altering goals or sensory features of the task, or adding interference tasks which may affect processes upstream to motor execution. If motor imagery depends on limited cognitive resources to form and maintain a representation during imagery, increased complexity should increase movement time compared to the overt group. However, if imagery involves forming a representation of the movement and then performing it via a simulation of the movement and assessing its error, complexity may not have a different effect on movement time between groups. Again, we hypothesized that imagery involves error-processing and therefore movement time would not differ between groups.

3.2. METHODS

3.2.1. Participants

We recruited 96 participants with normal or corrected-to-normal vision who self-reported having typical upper body sensorimotor function. Nine participants were removed from analysis due to technical issues with the experimental setup, resulting in a final data set of 87 participants. Participants were randomized into two groups with constraints to ensure roughly equivalent enrollment in each. The imagery group consisted of 43 participants, with a mean age of 23.2 years (SD = 4.74), 27 identifying as female; 6 were left-handed, and 1 was ambidextrous. The overt group consisted of 44 participants, with a mean age of 23.8 years (SD = 7.67), 32 identifying as female, and 2 were left-handed. Note that handedness was determined using the Edinburgh Handedness Inventory[31], and participants performed the experimental task with their dominant hand, with the single ambidextrous person choosing to perform the task with their right hand.

3.2.2. Experimental task

Participants performed a motor task designed to challenge execution of a kinematically complex, multi-articular upper extremity movement, the details of which have been described previously [19]. Briefly, participants sat at a 24” touchscreen monitor situated within a black box to reduce environmental distraction and ensure adequate contrast of the stimulus on the screen (Figure 2.1 A). Each trial consisted of a stimulus followed by a participant response. The study was performed in a single session with 6 blocks of 20 trials for a total of 120 trials. Imagery group participants performed 5 blocks of imagery trials with a final block of overt trials, and the overt group performed 6 blocks of overt trials.

Rest between trials was self-paced such that participants began a trial by tapping a button on the screen to begin the stimulus presentation. Stimuli depicted the movement pattern to be replicated by the participant, represented by a white dot that travelled from the starting position to four vertices before returning to the starting position. The starting position was always positioned in the bottom vertical (on the y-axis) half of the screen, with some variation depending on the pattern, and always centered horizontally (on the x-axis). The white dot made curved trajectories between each of the vertices, and always made a clockwise transition from vertex to vertex. Each stimulus pattern therefore consisted of five curved lines (see Figure 2.1 A). Stimulus patterns could therefore vary by the location of the vertices as well as the curvature of each trajectory between vertices, which gave rise to varying complexity. Complexity for a given trajectory was measured as its sinuosity, defined as the total pathlength of the trajectory, divided by the distance assuming each of the five lines were perfectly straight. Each participant was assigned one of five repeated trajectories (the movement to be practiced) that was presented at an equal ratio with randomly generated trajectories of similar complexity, resulting in 60 “repeated” and 60 “random” trials that were presented randomly but in equal proportions in each block. In either the repeated or random condition, the stimulus was animated in five different movement times (giving rise to varying speeds) in 500ms increments from 500ms (fastest) to 2500ms (slowest). Participants were asked to match both the movement trajectory as well as the speed of the movement on each trial. This allowed for performance to be assessed with a speed accuracy function.

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

3.2.3. Self-reported accuracy, actual performance, and expected performance

For both groups, immediately after each trial participants were asked “How accurate do you think your tracing was?” with a 10-point visual analogue scale where 10 represented perfect accuracy and 1 represented complete inaccuracy. After each block of imagery trials, participants were asked “How vivid was your motor imagery over the last 20 trials?” with another 10-point visual analogue scale where 10 represented perfectly vivid imagery and 1 represented not vivid at all. For each scale, participants responded by tapping the number representing their choice on the touchscreen. During overt trials, error was calculated as the mean of point-by-point Euclidean distance in millimeters (mm) between the stimulus and response trajectories. Both the stimulus trajectory animation and participant response trajectory were sampled at the touchscreen refresh rate of 60Hz, producing a timestamp and x and y coordinate for each sample. However, while the stimulus was animated at a constant speed, natural human movement does not unfold at a constant speed — that is, it is reasonable to expect participants to move faster along straight lines, slower along curves, and slowest around sharp corners. Therefore, dynamic time warping was used to optimally match response trajectories to stimulus trajectories to produce a time-invariant error measure [32]. To take into account the speed accuracy function [20], actual performance (that is, measured from physically executed movements during overt trials), was determined by dividing the mean speed by the mean error for each trial, thereby producing an intuitive positive number for “better” performance.

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

3.2.4. Statistical analysis

Bayesian hierarchical modelling was adopted to perform statistical inference in all analyses described below. For readers less familiar with Bayesian statistics we highly recommend the recent review by Kruschke and Liddell [33], and offer a technically imprecise but pragmatic interpretation of the 95% credible interval (from here on referred to as the 95%CI) as being similar to the frequentist 95% confidence interval, where for a given effect an interval that does not include zero can be considered “statistically significant”. Similarly, R^2 values with their own 95%CI can also be derived through Bayesian statistics[34]. For ease of interpretation, all variables were scaled to the observed data such that their mean value was zero and standard deviation was one. Here our Bayesian models used weakly informed priors equivalent to assuming the mean would fall somewhere within 10 standard deviations of the data observed. Analyses were carried out using the statistical software R, and all scripts can be found online (https://github.com/LBRF/DEMI_Analysis_Pipeline).

To test our first hypothesis that imagery participants will show a relationship between their self-reported accuracy and expected performance given the stimulus characteristics, we first built a model to predict expected performance. First, a hierarchical regression model was built such that the dependent variable was actual performance (which already took speed into account, as defined above), and independent variables including complexity, trial number, trial type (that is, whether the trial was for a repeated or a random pattern), and with participant included in a hierarchical fashion as a random variable. As our previous work using this experimental task demonstrated that performance improves on repeated trials relative to random [19], we included an interaction term for trial number and trial type. This model was fit using all overt trials, including all trials from the overt group and the final block of the imagery group. This model was also used as a manipulation check to ensure actual performance improved across trials on the repeated relative to the random pattern.

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

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

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

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

3.3. RESULTS

3.3.1. Self-reported accuracy is correlated with expected performance

Regression analyses demonstrated that actual performance improved across time in repeated relative to random trials (see Figure 3.1), but this interaction effect was small and credibly included zero (Cohen's *d* = .04, 95%CI -.01 to .09. This finding is in line with our previous work with this experimental paradigm that changes within session are modest but become material across multiple sessions [19]. Complexity had a small negative effect on actual performance (Cohen's *d* = -.08, 95%CI -.11 to -.06).

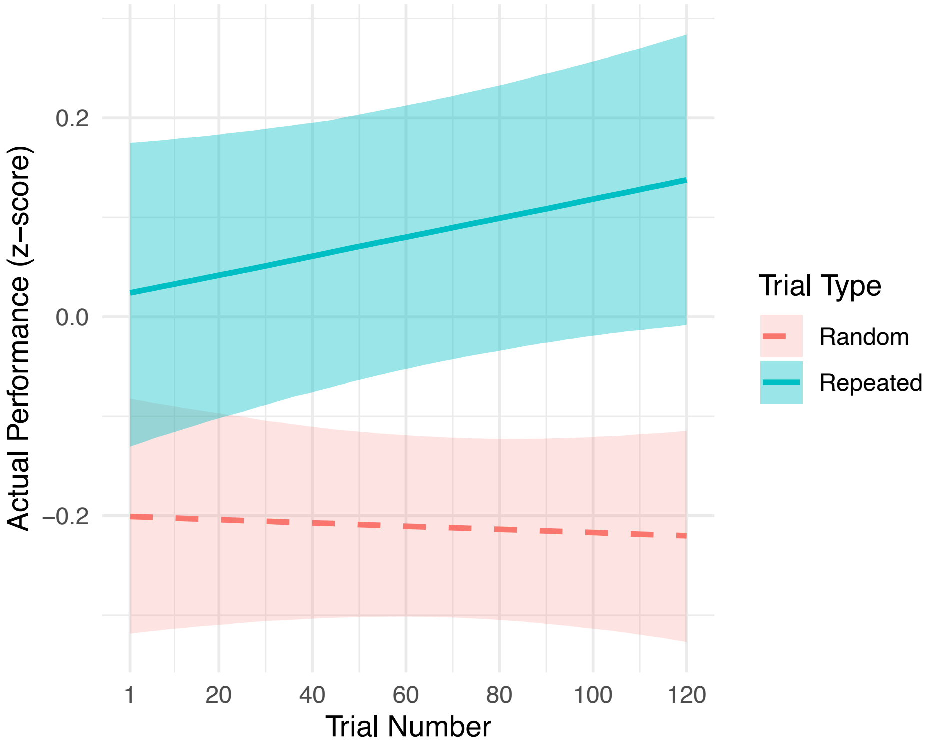

Figure 3.1. Conditional effects of trial number by trial type (repeated versus random) on actual performance during overt trials. Lines represent mean and ribbons depict 95% credible interval as estimated by the regression model, not including random effects for clarity. Actual performance z-scored to aid in interpretation.

The first model was used to predict expected performance on all trials (both overt and imagery) to allow for subsequent regression analyses. As a manipulation check, we first investigated whether self-ratings of accuracy correlated with actual performance. Indeed, self-rated accuracy and actual performance positively correlated with an R^2 of 0.48 (95%CI: 0.46 to 0.49) which validated that self-reported accuracy was a sensible measure to use for subsequent analyses. Next, we used regression analyses to investigate the correlation between self-reported accuracy and expected performance in each group separately. In the overt group, self-reported accuracy was positively correlated with expected performance ($R^2 = 0.51$; 95% CI: 0.50 to .52). Similarly, in the imagery group, self-reported accuracy was also positively correlated with expected performance but with a slightly weaker relationship ($R^2 = 0.45$; 95% CI: 0.44 to 0.47). A subsequent regression adding self-reported vividness ratings explained an insignificant amount of additional variance ($R^2 = .47$; 95% CI: 0.46 to 0.49) and demonstrated that vividness had only a small effect on self-reported accuracy (Cohen's $d = .20$; 95% CI: .11 to .29) compared to the large effect of expected performance (Cohen's $d = .97$; 95% CI: .64 to 1.31) and the two factors did not interact (Cohen's $d = .08$; 95% CI: -.09 to .26). Importantly, while the R^2 values were different between groups, a subsequent regression that included both groups demonstrated that the positive slopes (that is, the beta coefficients for the group by expected performance interaction) were not significantly different between groups (Cohen's $d = .07$, 95%CI = -.13 to .29). However, there was a significant main effect of condition indicating that subjects performing imagery rated their accuracy higher (Cohen's $d = .51$, 95%CI = .36 to .65; Figure 3.2). These results suggest that participants performing motor imagery are capable of imaging movements with a level of performance aligned with the demands of the task (e.g., the speed and complexity) and their experience with the movement (e.g., trial number and type).

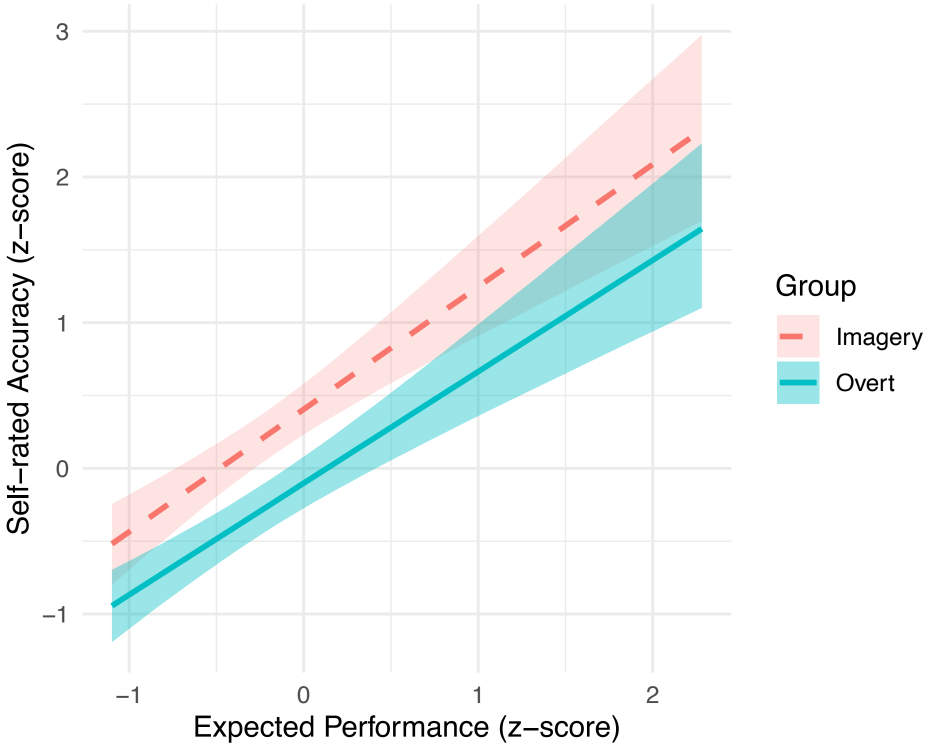

Figure 3.2. Conditional effect of expected performance on self-reported accuracy for each group. While imagery participants rate their accuracy higher in general, self-reported accuracy is correlated with performance expected given the characteristics of the trial, including the movements complexity, speed, and familiarity (whether the trajectory was repeated or not, and when in the experiment the trial occurred). Lines represent mean and ribbons depict 95% credible interval as estimated by the regression model, not including random effects for clarity. Z-scores presented to aid in interpretation.

3.3.2. Self-reported accuracy improves with experience

Next, we investigated whether self-reported accuracy changed across time and whether this was different between the overt and imagery groups (Figure 3.3). Regression analyses demonstrated a significant interaction between trial number and trial type, where repeated trials improved (i.e., self-reported accuracy increased) while random trials did not (Cohen's *d* = .10, 95%CI = .05 to .14). There was a main effect of condition, where participants reported greater accuracy during imagery compared to overt trials (Cohen's *d*

= .58, 95%CI = .45 to .71). Importantly, there were no significant interactions between condition and any other factor — including a lack of a three-way interaction between condition, trial number and trial type (Cohen's *d* = -.04, 95%CI = -.12 to .04). These results suggest that imagery is capable of creating a never before experienced movement representation and updating it with repeated practice, improving accuracy as one would expect during training that occurs through overt practice.

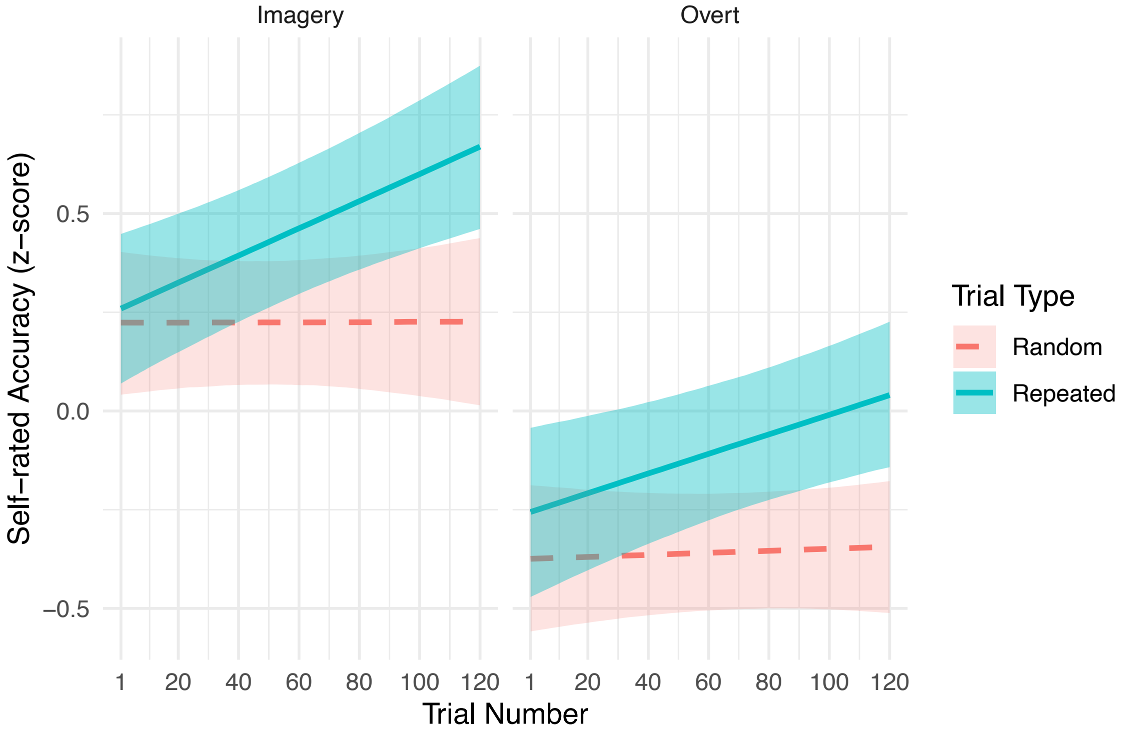

Figure 3.3. Conditional effects of trial number by trial type (repeated versus random) on self-reported accuracy for each group. The imagery group consistently rated their accuracy higher but demonstrated the same relationship with explanatory variables as the overt group, demonstrating that repeated movement patterns improved across trials compared to novel (random) movement patterns. Lines represent mean and ribbons depict 95% credible interval as estimated by the regression model, not including random effects for clarity. Self-reported accuracy presented as z-score to aid in interpretation.

3.3.3. Kinematic complexity did not influence imagery movement time

Next, we investigated whether kinematic complexity had a different effect on each group with respect to their ability to match their movement time to the animation time of the stimulus. Regression analysis demonstrated that generally participants matched their movement time to the stimulus movement time well (R^2 of whole model: 0.76; 95% CI: 0.76 to 0.77) and the main effect of stimulus movement time on response movement time was large and significant (Cohen's d = .72, 95%CI = .68 to .76). However, this was the only significant effect in the model. Importantly, the interaction between complexity and stimulus movement time was not significantly different between imagery and overt conditions (Figure 3.4). That is, complexity did not have an effect on participants ability to match their movement speed to the task requirements during imagery or overt trials. Furthermore, there was no main effect of condition, suggesting that imagery trials did not take longer than overt trials. Finally, there was no main effect of complexity, suggesting that increasing complexity did not lead to longer movement times. Therefore, movement time was strictly a function of the stimulus animation time in during both overt and imagery trials.

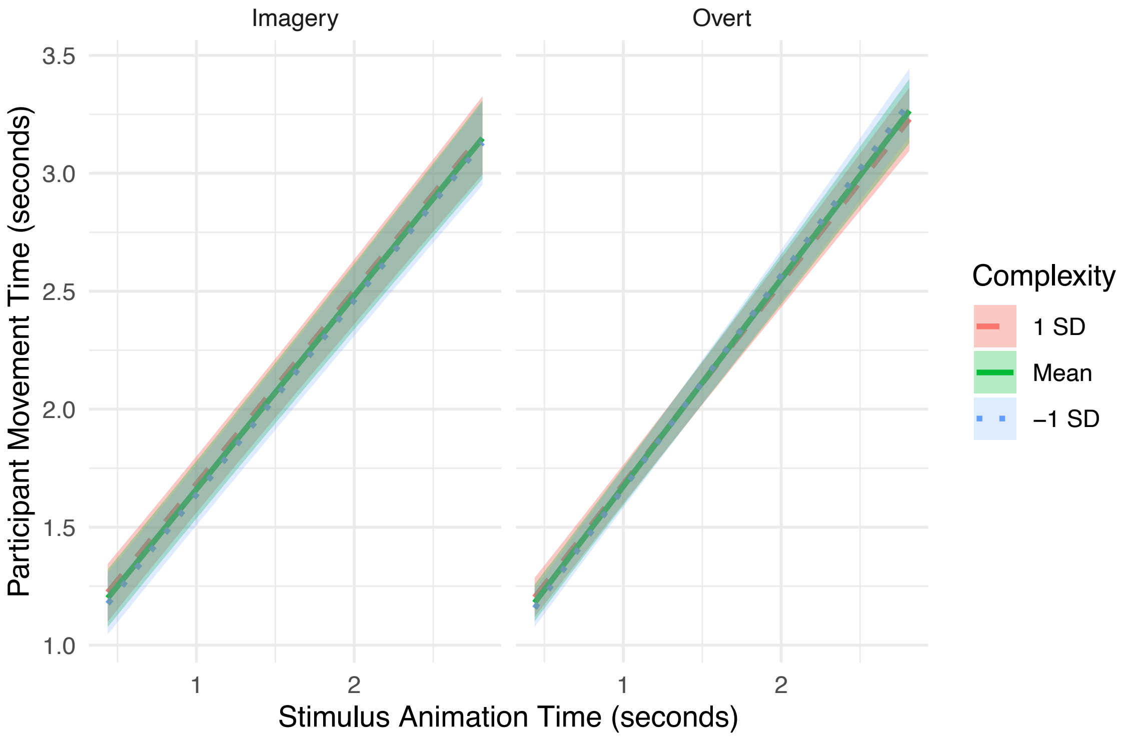

Figure 3.4. Conditional effects of stimulus animation time on participant movement time for varying levels of complexity for each group. Figure depicts mean complexity observed, mean + 1 SD, and mean - 1 SD. For both groups, movement time was a function of stimulus animation time only, and not affected by complexity. Lines represent mean and ribbons depict 95% credible interval as estimated by the regression model, not including random effects for clarity.

3.4. DISCUSSION

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

This experiment adds to the growing literature that motor imagery makes use of internal models [24], namely a forward model to predict the sensory consequences of the imagined movement [27], despite never experiencing the actual sensory consequences. This may explain why motor imagery is capable of driving motor learning of novel motor skills in the absence of sensory feedback [19,35]. While motor imagery lacks sensory feedback necessary to derive an error signal between the observed effects and the intended or predicted effects, imagery may involve the creation of forward models that allow for a comparison between the intended and predicted effects of the imagined movement [24]. Repeated imagery may therefore allow for refinement of the forward model or movement representations that depend on it to reduce the difference between the intended and predicted effects. It is likely that actual sensory effects provide more detailed error information, which explains why imagery participants rated their accuracy higher in general throughout the experiment. The lack of additional error information also explains why motor imagery is typically less effective than overt practice for driving performance improvements [17,19,20,35–38].

Our results differ from those predicted by theories of motor imagery that posit a lack of involvement by the motor system. Our finding that task complexity did not influence imagery movement times is in opposition to the motor-cognitive model [2]. We suggest that our results are less surprising when considering the nature of the experimental task used in the present study. Here we used a task that emphasizes motor execution (whether performed overtly or via imagery) and de-emphasizes upstream processes such as perceptual processing, goal selection, and motor planning [12]. While it is likely impossible to completely isolate any one of these processes — they all operate to some degree in parallel — we contend that many experimental manipulations in the motor imagery literature are biased to have their effects on processes other than motor execution. For example, tasks that measure performance using reaction time are likely explained by improvements in perceptual processing of stimuli, goal selection and motor planning, but not improvements in the quality of the movement itself. Similarly, many motor tasks involve experimental manipulations that require online goal selection and motor planning during the movement — for instance, a change to the task requirements during execution (e.g., changing a cursor position to require a correction mid-movement), or the movement requirements are not completely specified until the movement is in progress (common in forcefield paradigms), or an interference task is introduced during the movement. In each case, parallel perceptual processing, goal-switching, and motor plan updates can disrupt the ongoing or subsequent movement. In the present paper complexity was operationalized as a feature of the movement itself and was not altered once the participant began imagining the movement. Our results imply that once a motor command is ready to be performed, the amount of time needed to imagine it is not affected as long as the participant is allowed to bring the movement to completion without making any additional decisions. However, while our results do not support the motor-cognitive model, they also do not support the alternative motor simulation theory and the notion of functional equivalence. Participants rated their accuracy as significantly higher during imagery compared to overt trials, and our previous work with this experimental task demonstrated that overt training is superior to imagery for driving motor learning [19]. What's more, despite our results with respect to complexity, we agree that the literature supports the suggestion by the motor-cognitive model that motor imagery requires greater executive resources [2], and point to additional literature demonstrating that imagery has a greater reliance on perceptual processing in SRT tasks [17], imagery more readily encodes effector independent information and may not encode effector dependent information at all [37], and imagery appears to drive skill learning through different acquisition and consolidation processes compared to overt practice [20].

It is possible the greater demand imagery imposes on cognitive resources is multi-factorial, and particularly due to the challenge of performing a simulation along with the need to inhibit overt movement. Overt movement involves online feedback control whereby the unfolding movement considers both an evolving forward model and sensory information in real time [39,40]. Movement simulation via imagery may be afforded forward models but there is no sensory information. Online control during movement simulation therefore may rely more on the generation of sensory consequence predictions rather than simply receiving this information from the environment, which may require additional processing. Indeed, neuroimaging studies have demonstrated that imagery more consistently involves activation of parietal structures implicated in sensory integration and spatial processing [41,42], patients with parietal lobe damage are impaired in their ability to perform imagery [43–45], and imagery-based motor learning is disrupted by inhibitory brain stimulation to these parietal areas [46]. Another challenge in performing motor imagery may involve the inhibition of overt movement while utilizing the motor system to perform the simulation [47]. The motor-cognitive model posits that for many tasks motor imagery is more susceptible to disruption (e.g., longer movement times) than overt movement because the motor representation is formed and elaborated upon through executive resources. While it is true that frontal cortical regions such as the dorsolateral prefrontal cortex are more consistently active during imagery than overt movement [3], and that these areas have been implicated in executive functioning [48], it is also true that they have been implicated in inhibition [49], and it is possible that increasing working memory demands (as per interference tasks) disrupts inhibitory function [50,51].

That motor imagery is capable of using forward models to perform a comparison between predicted and intended movement provides evidence that imagery involves the motor system. However, it raises several additional questions. What is the nature of “error” in a motor simulation? When an amateur artist attempts to paint a landscape, it is unlikely that they consider the deficiencies in their work “errors” — it’s not a slip of their brush, but a lack of ability to reproduce the image they intend to. Our work demonstrates that imagery is afforded a sense of accuracy, but it does not necessarily prove that simulations produce errors that are then detected and processed as per overt movement. We propose that motor imagery engages much of the motor system but with important additions and omissions. Obvious differences include the lack of overt movement, which may be reflected in the lack of consistent primary motor cortex activation across neuroimaging studies [3], given its critical role in executing skilled movement [52]. As premotor and parietal motor areas are consistently activated during motor imagery — sometimes more so than during overt movement [3] — motor imagery may involve much the same perceptual processing and motor planning as during overt movement, but with additional movement inhibitory processes as well as greater demands on sensory feedback predictions. We contend that during imagery sensory predictions are used to inform the evolving forward model in the absence of sensory feedback, resulting in iterative use of prediction which may compound uncertainty as a given trial of imagery unfolds. While this certainly increases cognitive processing demands of imagery compared to overt practice, the human motor system is nonetheless capable of performing these simulations, as if to test and iterate over a motor plan without ever physically experiencing it. As such, a fertile area of future investigation might be developing more sophisticated behavioural tasks that interrogate the computations underlying successful motor imagery and their neurophysiological correlates — which is indeed an active area of investigation in the study of motor control generally [53–56].

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CHAPTER 4 | NEUROPHYSIOLOGICAL CORRELATES OF ACCURACY DURING AND AFTER IMAGINED MOVEMENT EXECUTION

4.0. ABSTRACT

Whether imagined movements involve the processing of accuracy in a similar manner as overt movement error-detection is a subject of debate with implications for imagery-based motor learning and the practical applications thereof. We sought to investigate the neurophysiological correlates of imagined movement accuracy and familiarity and contrast them with those observed during overt movement. Participants assigned to either motor imagery (MI) or overt movement (OM) had electroencephalography (EEG) recorded while performing a motor task focused on challenging motor execution of either repeated (familiar) or random (unfamiliar) movements. Movement accuracy was self-reported by participants of both groups and validated to relate to actual error using OM trials. Generalized additive models were used to determine which sensors demonstrated accuracy or familiarity related theta, alpha and beta frequency changes both during and after imagined or overt movement. As expected, our results largely replicated previous OM findings that low accuracy (i.e., error) is associated with increased power in theta over frontal regions and decreased power in alpha over posterior parietal regions. MI differed markedly in that low accuracy was related to decreases in power in theta over frontal regions and decreased power in alpha over posterior parietal regions only when movements were familiar, whereas unfamiliar movements led to a decrease in power in alpha over sensorimotor and bilateral parietal regions. Taken together, our results demonstrate that MI indeed involves processing of

imagined movement accuracy, and that this processing recruits similar brain regions as OM but with different neurophysiological features.

4.1. INTRODUCTION

Motor imagery — the mental rehearsal of movement — has been shown to drive motor learning [1], sparking considerable interest in its potential use in neurological rehabilitation [2–4]. Despite a growing body of literature, the underlying mechanisms of motor imagery are poorly understood. Many of the challenges of studying motor imagery are rooted in its covert nature. That is, investigators of motor imagery have few behavioural outputs to measure given that overt movement does not occur. Instead, studies often rely on studying the effects of their experimental manipulations on the duration of imagined movements [5,6], or investigating performance changes in overt movement before and after imagery [1]. Neuroimaging techniques offer a compelling tool for making inferences about the processing involved during imagery [7,8], but the data collected with these technologies are still limited by the behaviours they can be correlated with. Given the difficulties inherent in studying motor imagery, it is not surprising that theories accounting for its underlying mechanisms differ considerably.

Theoretical frameworks of motor imagery often involve comparisons with overt movement. One prominent theory known as motor simulation theory posits that motor imagery involves the same processes as overt movement — including "functionally equivalent" neural mechanisms — but without the occurrence of overt movement [5,9,10]. Modern interpretations of motor simulation theory elaborate on why movement is absent during imagery (e.g., inhibitory mechanisms)[11], and what happens during that absence (e.g., an internal simulation of the movement and its sensory consequences)[5,12]. Motor simulation theory has recently been directly challenged by the motor-cognitive model [6]. The motor-cognitive model posits that motor imagery and overt movement share pre-movement motor planning processes but diverge upon motor execution, where imagery is unable to avail to unconscious and automatic motor processes. Instead, motor imagery becomes an executive process requiring greater cognitive resources compared to overt movement to form and elaborate an image of the movement. In addition to these contrasting theories, experiments show that the differences and similarities between motor imagery and overt movement appear to be subtle but important. For instance, experimental work has demonstrated that compared to overt movement, motor imagery appears to rely more on perceptual processing [13], more readily encodes effector independent information about a movement [14], utilizes different acquisition and consolidation processes when driving motor learning [15], and is generally less effective at driving motor learning [16–18]. However, an important similarity with overt movement is that motor imagery appears to be capable of utilizing forward models that predict the sensory consequences of the imagined movement [19]. That motor imagery utilizes forward models may provide an explanation for why motor imagery is capable of driving motor learning in the absence of an error signal provided by movement related sensory feedback [16]. That is, it is possible that an error signal may be derived from a comparison between the intended outcome of a movement and the predicted sensory outcome of a movement simulated via imagery [20]. However, there remains little experimental data about the content of imagined movements and whether or not error-related information is produced during imagery or if a comparative process exists (i.e., a comparison between predicted and intended sensory effects of the movement) [5,20].

Literature exploring the neurophysiological basis of error processing during overt movement may provide insight into how error factors in motor imagery. To date, extensive neuroimaging work has demonstrated only limited support for either motor simulation theory or the motor-cognitive model, showing both similarities and differences between motor imagery and overt movement [7,8,21]. While both overt movement and motor imagery appear to activate premotor areas (PMA; including the supplementary motor area (SMA)), imagery more consistently involves pre-SMA while overt movement involves SMA proper [8,22]. Activation of parietal cortex during overt movement is anteriorly shifted toward primary sensory cortex, while motor imagery tends to activate posterior parietal cortex (PPC) [7,8,22]. While both overt movement and imagery recruit frontal cortical areas, imagery appears to more consistently recruit dorsolateral prefrontal cortex (DLPFC) [7,8,22,23]. Supporting the idea that forward models are involved in imagery, the cerebellum is involved in imagery but appears more caudal and less somatotopically organized than during overt movement [8,23]. However, neuroimaging literature tends to focus only on correlating brain activation (e.g., using functional magnetic resonance imaging; fMRI) with the performance of either motor imagery or overt movement, and rarely on experimental manipulations of either. What's more, when two tasks activate the same brain region, it does not imply that the same processes are occurring in that brain region [24,25]. While subject to its own limitations (e.g., spatial resolution), frequency-based analysis of electroencephalography (EEG) data offers additional information beyond whether a particular region is active or not, as it allows for measurement of relative changes (increases or decreases) in oscillatory brain activity in several different frequency bands at a given location. That is, when a particular brain region is activated during both overt movement and motor imagery, this activation may involve increases or decreases of oscillatory activity in different frequency bands, which may provide evidence of different neural processes. EEG also offers the temporal resolution necessary to study more discrete movements with short movement times, which is often the case when experimental tasks are designed for studying movement error. As an example, EEG frequency analyses have demonstrated that when motor tasks are manipulated to differently challenge motor control and sustained attention, changes in oscillatory activity in both frontal and parietal regions are observed but at different magnitudes [26]. Specifically, motor task errors attributable to failures of motor control result in greater increases in theta band (4-8 Hz) power over frontal regions, whereas errors attributable to lapses in sustained attention result in greater decreases in alpha band (9-12 Hz) power over PPC [26]. As some theories claim that frontal activation during motor imagery may be related to either attention and working memory demands [6], or inhibition of overt movement [5], investigating how these neural signals relate to motor task error during imagery is of interest. While motor task error has also been associated with suppression of sensorimotor post-movement beta (13-30 Hz) power increase (or “synchronization”; PMBS) [27], the PMBS has since been shown to more readily represent uncertainty in the motor system — that is, greater PMBS is associated with less weighting on sensory prediction errors and greater confidence in the existing forward model [28,29], as though the increase in beta power represents a decision to discount sensory feedback and maintain the forward model. Finding a similar phenomenon in motor imagery would support the notion that imagery involves a comparison between the intended movement outcome and predicted outcomes. While literature certainly exists investigating motor imagery using EEG (or magnetoencephalography) [30–32], we are not aware of any EEG studies investigating motor imagery error processing and how it may differ from the results observed for overt movements.

Here we report a study exploring questions about motor imagery accuracy using EEG. We used a previously established motor task designed to induce error due to faults in motor execution rather than faults in perceptual processing [16]. EEG data from 30 sensors (not including reference, mastoid, or ocular channels) was collected while participants performed kinematically complex movement patterns on a touchscreen either overtly or via motor imagery. As participants may process error differently based on their confidence in a forward model (as per the PMBS literature cited above), movement patterns were either repeated and therefore familiar, or randomly generated and therefore unfamiliar. Error was manipulated by varying speed to induce a speed accuracy tradeoff [33,34]. As movement error cannot be measured during motor imagery, we asked participants in both imagery and overt groups to self-report their accuracy after every trial. Importantly, we validated that these self-reports are well correlated with actual performance (e.g., error) in all participants, and are largely driven by characteristics of the movement (e.g., speed, complexity, and familiarity) rather than vividness of imagery (see Chapter 3). This experimental setup allowed us to assess the relationship between the neurophysiological data during low accuracy (conceptually similar to high error) or high accuracy (low error) trials in both familiar and unfamiliar movements, and during both overt movement and motor imagery conditions. Given the existing literature on error processing in overt motor control discussed above, we constrained our analyses to power in the theta (4-8Hz), alpha (9-12Hz), and beta (13-30Hz) frequency bands. For each frequency band we assessed power changes from baseline during the movement as well as immediately after the movement ended. Given the large possibility space — changes in EEG in 2 groups, 30 sensors, 3 frequency bands, 2 epochs, 2 task conditions, and accuracy as a continuous variable — we took an exploratory approach to our analysis and used a conservative approach to inference (see 4.2.5 Statistical Analysis). As such, we opted to use Generalized Additive Models as they are highly interpretable yet allow for rich modelling of nonlinearities in variables, including random effects, and convenient spatial modelling (in this case including the relative three dimensional location of each channel), with a wide exploration of the parameter space with regularizing penalty terms to avoid overfitting [35].

While the analysis was exploratory in nature, we hypothesized that our results would largely replicate previous findings in the overt movement group. Specifically, we hypothesized that the overt group would demonstrate error (low accuracy) related frontal theta power increases during movement, and error related posterior parietal alpha power decreases after movement. Furthermore, we hypothesized that the overt group would demonstrate a familiarity related (during repeated pattern trials compared to random) sensorimotor beta power increase (the PMBS) after movement. Given the previously described evidence that imagery may involve error processing but without the use of sensory feedback, we hypothesized that both accuracy and familiarity related changes in EEG power will be represented differently in the imagery group. Specifically, we hypothesized that like the overt group, the imagery group would demonstrate error related frontal theta power increases during imagined movement, error related posterior parietal alpha power decreases after imagined movement. However, unlike the overt group, we hypothesized that the imagery group would not demonstrate a familiarity related PMBS after movement given the lack of sensory feedback. Note that we did not constrain our interpretation of the results to these specific hypotheses and opted to discuss all noteworthy results.

4.2. METHODS

4.2.1. Participants

The participants recruited for this experiment were the same as those recruited for the work presented in Chapter 3. We recruited 96 participants but 16 were removed from analysis due to technical issues with the experimental setup. Participants were pseudo-randomized to ensure roughly equivalent enrollment in each group, resulting in the overt movement (OM) group consisting of 41 participants and the motor imagery (MI) group consisting of 39 participants. The MI group had a mean age of 23.1 (SD = 4.44), 25 self-identified as female, and 4 were left-handed and one was ambidextrous as measured by the Edinburgh Handedness Inventory [36]. The OM group had a mean age of 23.8 (SD = 7.79), 30 self-identified as female, and 2 were left-handed. Participants were asked to perform the task described below with their dominant hand, and the ambidextrous individual chose to perform the task with their right hand.

4.2.2. Experimental Task

The experimental task was designed to challenge execution of a kinematically complex, multi-articular unilateral upper extremity movement, which was described in detail in Chapter 2 [16]. Briefly, after EEG setup was complete (described below), participants were seated in front of a 24” touchscreen monitor (Figure 2.1A). For each trial the stimulus consisted of a target trajectory that animated to completion before the participant was asked to replicate it with their index finger using the same touchscreen upon which the stimulus was presented. The stimulus was animated using a white dot that travelled from a starting position that was located at the center and near the bottom of the screen. The white dot travelled in curved trajectories, connecting with four vertices before returning to the starting position, resulting in a pattern that consisted of five curved lines (see Figure 2.1). Variation was present in both the location of each vertex (except for the starting position) and the curvature of the path between them, which produced trajectories of varying complexity. Trajectory complexity was measured by sinuosity; that is, the total pathlength of the curved trajectory divided by what the pathlength would have been if each vertex-to-vertex line was straight. Trajectory speed varied by animating them at one of five different movement times (500, 1000, 1500, 2000, and 2500ms). Each participant was assigned one of five trajectories that repeated throughout the experiment (the 'repeated' condition), which was interspersed with an equal proportion of randomly generated trials of similar complexity (the 'random' condition). Each 20-trial block consisted of 10 repeated and 10 random trajectories, presented pseudo-randomly to ensure equal exposure of each condition as well as equal exposure of each movement time. Participants performed 6 blocks for a total of 120 trials in the experiment.

After each stimulus the participant was asked to replicate the trajectory as accurately as possible. A speed-accuracy trade-off was induced by asking participants to match the speed at which the stimulus was presented. This resulted in a motor task that consistently resulted in error regardless of the level of familiarity with the trajectory [16]. Importantly, this was not a reaction time task — both the initiation of the trial and the beginning of the response was self-paced. Once a stimulus trajectory was complete the starting position became highlighted as a red circle, and upon placing a finger at the starting position the circle immediately changed color to green indicating that the trial had begun, and the response was “recording”. Once the participant returned to the starting position the green circle disappeared, marking the end of the trial. Importantly, no additional visual feedback was presented to the participant — that is, the stimulus was not presented as a tracing during or after the trial, and the participants response was also not shown. The MI group performed the same procedure with the exception that upon placing their finger on the starting position, they were instructed to simply imagine performing the movement and lift their finger off the green circle once they were complete, thus indexing MI movement time in the same manner as the OM group. MI participants were familiarized with the concept of kinaesthetic imagery (e.g., told to imagine what the movement would look like as well as what it would feel like). Note that the MI group performed imagery during the first five blocks but performed the task overtly in the sixth block, whereas the OM group performed overtly in all six blocks.

4.2.3. Performance, Accuracy, and Vividness

Stimulus and response trajectories were both sampled at the refresh rate of the touchscreen monitor (60Hz), resulting in an ordered series of points with a timestamp, and x and y coordinates. Error was then calculated as the mean point-by-point distance between the two trajectories in millimeters (mm). Importantly, stimulus trajectories were animated at a constant speed. This is not a reasonable expectation for human movement where participants tend to slow down around corners and speed up on straight lines. Therefore, we used dynamic time warping to match response trajectory points to optimally corresponding stimulus trajectory points to produce a timing-invariant error measure [37]. Given the task involved a speed-accuracy trade-off [34], actual performance was finally determined for each overt trial by dividing the mean speed by the mean error (rather than dividing error by speed [15]) to produce a measure of performance where a greater positive number represented greater accuracy.

Immediately after each trial participants were asked “How accurate do you think your tracing was?” and responded using a 10-point visual analogue scale where 1 meant not accurate at all and 10 meant perfect accuracy. This question was presented after both overt and imagery trials. For imagery trials only, each 20-trial block ended with the question: “How vivid was your motor imagery over the last 20 trials?” where participants again responded using a 10-point visual analogue scale where 1 meant not vivid at all and 10 represented perfectly vivid imagery. The relationship between self-reported accuracy and actual performance was then assessed using overt trials (including the sixth block of the MI group) by performing regression analysis with self-reported accuracy as the independent variable and actual performance and vividness rating as the dependent variables. Results are reported in detail in Chapter 3. Briefly, actual performance had a significant and large effect on self-reported accuracy, whereas vividness rating had only a small effect that explained only a negligible amount of additional variance. These results validated self-reported accuracy as a sensible proxy for performance accuracy during motor imagery.

We opted to describe our results below in terms of accuracy, rather than error. During piloting, the concept of error during motor imagery was difficult to articulate to participants — that is, asking for self-ratings of error, such as “how much error occurred during that trial?" was interpreted as confusing and unnatural. Error was understood as either being binary (e.g., hit or miss), a count (e.g., number of misses), or having a unit to describe magnitude (e.g., distance from target in mm). The latter two might apply to the current experimental task but pilot participants had difficulty reporting such measures during either OM or MI. Finally, the concept of error during motor imagery is difficult to conceptualize. Using the analogy of an amateur painter attempting to recreate a scene, it is unlikely the painter would attribute poor quality as "error" but as a lack of their ability to recreate the scene accurately. Whether bouts of motor imagery include "error" or are simply more or less accurate is beyond the scope of the current investigation.

4.2.4. Electroencephalography (EEG)

EEG data was collected using a 32-channel QuikCap setup (Compumedics Neuroscan, Charlotte, NC). In addition to EEG, electrooculography (EOG) data was collected to allow for the removal of artefacts resulting from eye movements. EEG data was acquired continuously throughout each session at a sampling rate of 1000 Hz and a band-pass of DC-500 Hz (SynAmps RT, Compumedics Neuroscan, Charlotte, NC) and stored for offline analysis. During data collection the experimental software 'marked' the continuous EEG data to allow for precise epoching during subsequent analysis, including the start and end of each stimulus trajectory, and the start and end of each response trajectory. This was achieved through an interface of the (behavioural) experiment software on an iMac connected to the touchscreen monitor and the EEG system via a USB-based LabJack system.

Pre-processing of the EEG data was completed using the open-source software MNE-python [38,39], and specifically a standardized early-stage EEG pre-processing pipeline [40]. Briefly, the standardized pipeline first removes line-noise, robustly references the signal to an estimate of the true average reference, detects bad channels relative to this reference, and optionally interpolates these bad channels — importantly, we opted not to interpolate bad channels and simply removed them from analysis. High-pass (1Hz) and low-pass (50Hz) filters were then applied ahead of the removal of EOG artefacts by performing independent components analysis using the Picard method [41]. To reduce the effects of volume conduction [42], data were then spatially filtered using the current source density approach.

The remaining processing was completed using the statistical software R [43]. EEG data was down sampled to 100Hz to facilitate computation while avoiding aliasing given that the highest frequency of interest was 30Hz (the upper bound of the beta frequency band). Two epochs were taken from each trial such that the first epoch ("during movement") was time-locked to the beginning of the participant response (overt movement or imagery) and the second epoch ("after movement") was time-locked to the end of the response and thus represented time immediately post-movement. Both epochs were 1 second in length with the addition of 1 second of padding before and after to reduce the risk of edge effects after time-frequency decomposition. While one fifth of trajectory animation times were 500ms (the fastest trials) we observed that participants rarely responded with a movement less than 1 second in length. Therefore, one second epochs were used to ensure that the first ("during movement") epoch always captured movement (or imagery) from each trial regardless of the speed of that trial. To aid in visual inspection of the processed EEG data, each epoch time series data was then decomposed into time-frequency representations at 1 Hz intervals from 1 Hz to 48 Hz using a continuous wavelet transformation with the Morlet wavelet as the mother wavelet [44]. Given that each trial involved participant movement to initiate a new trial and respond (e.g., reaching for the starting position), time-frequency power was decibel normalized using a baseline period of -500ms to -200ms before the end of the stimulus presentation to reduce the risk that the baseline was taken while participants were moving. Pilot testing with electromyography demonstrated this to be the most reliable portion of a trial in which participants were at rest, but it should be noted that this baseline likely includes visual and perceptual processing of the stimulus — but we felt this was acceptable given the focus of this experiment on movement (or imagined movement) related EEG. Reference electrodes located over the mastoid process bilaterally were removed for plotting and statistical analysis. Mean processed EEG data across all trials for a representative participant in the overt group is presented in Figure 4.1, and grand mean for each group is presented in Appendix A (where left-handed participants have had their sensor coordinates mirrored).

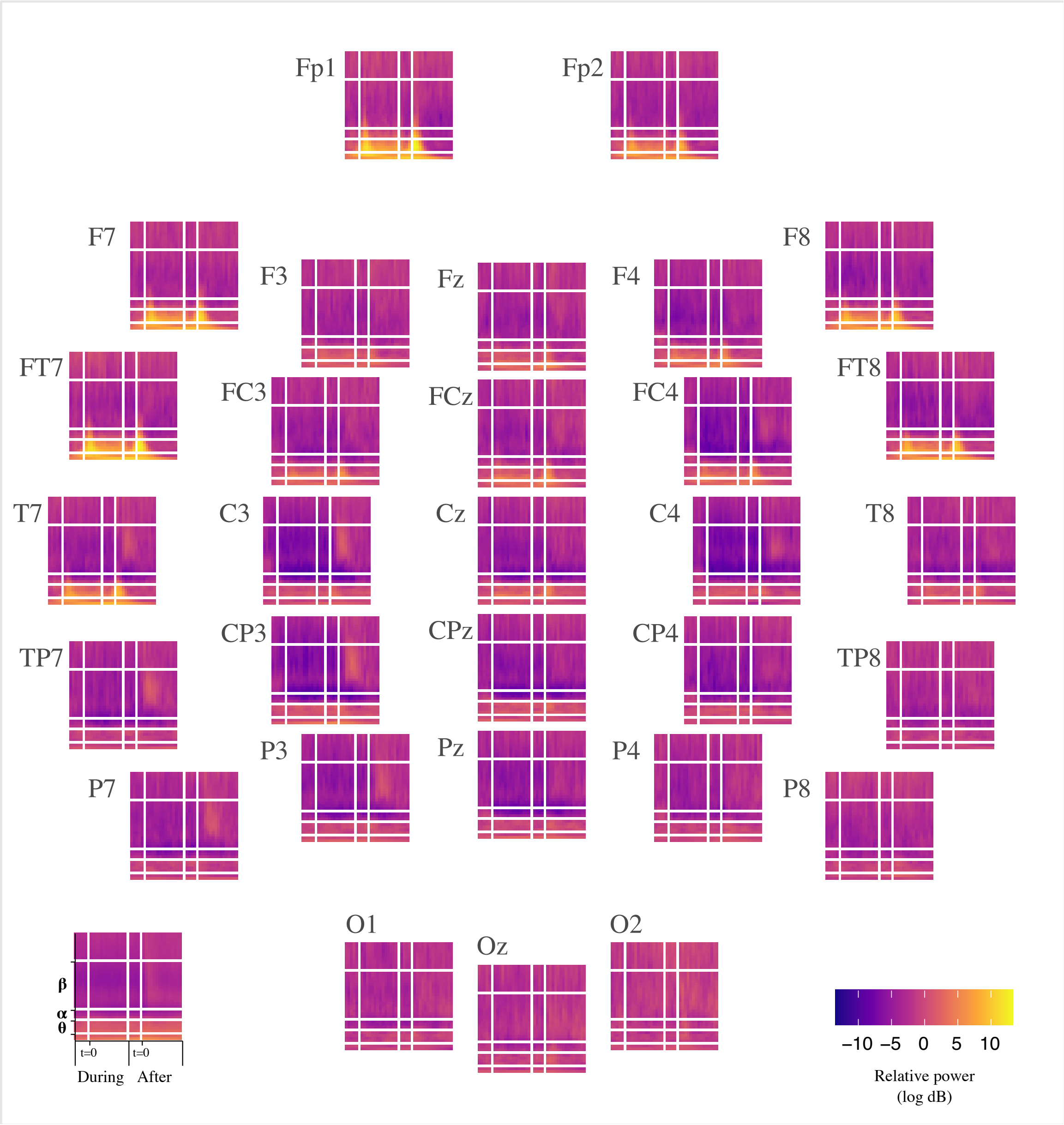

Figure 4.1. Mean EEG across all trials for a representative participant of the OM group. As specified by the label key (bottom left), plot include all frequencies from 1 to 40 Hz including the bands of interest: theta, alpha and beta, as well as time ranging from 0.5 seconds before movement onset (the first t = 0) and 1.5 seconds thereafter (epoch 1; during movement), and 0.5 seconds before movement cessation (the second t = 0) and 1.5 seconds thereafter (epoch 2; after movement). This participant demonstrates several well-known movement and motor error related EEG features described in the literature, including sensorimotor (most prominent at C3) beta power decrease during movement, and power increase post-movement, and frontal theta power increase during movement. EEG is presented as decibel normalized power on the range of the scale key (bottom right).

4.2.5. Statistical Analysis

Statistical analysis was performed using a hierarchical generalized additive model [35]. First, mean power was computed across both time and frequency for each trial, frequency band, epoch, sensor location, trial type (i.e., repeated or random), and participant. Sensor location was represented as a location on a sphere using latitude and longitude coordinates, and left-handed participant sensor locations were mirrored, (i.e., C3 location was converted to C4 location). This yielded the dependent variable that could then be predicted by a model including each of these variables as well as a self-reported accuracy rating for each trial. The model was specified such that any factor with only two or three levels was treated as they would for a linear model, including all possible interactions. Specifically, these factors were specified as half sum contrasts and included group (OM and MI), band (theta, alpha, and beta), epoch (during movement and after movement) and trial type (repeated and random). Inference for main effects and interactions involving the continuous variables was achieved through a generalized additive model with a "splines on a sphere" representation of electrode location and cubic spline representation of self-reported accuracy, with complexity parameters for these possibly-non-linear effects set to the maximum (n.b. this parameter sets the maximum complexity to be explored by the model, which will then seek out the degree of complexity best supported by the data, including the possibility of linear and zero effects). Finally, participant was included as a random effect on the intercept.

Our approach to inference involved deriving from the fitted model a predicted mean power change (from baseline) and 95% confidence interval for comparisons of interest (e.g., high and low self-reported accuracy in each epoch; see Figure 4.2 as an example) at each sensor location, and where high accuracy referred to the upper quintile (top 20%) of accuracy ratings and low accuracy the lower quintile. This binarization of the accuracy measure aided in interpretation of our results with previous literature, where EEG results are typically reported as being “error-related” (in our case, low accuracy compared to high accuracy). Non-overlapping confidence intervals denoted a significant effect — that is, either 1. the confidence interval of a given effect not overlapping with zero (for example, when indicating a significant sensorimotor beta power decrease from baseline during movement) or 2. the confidence bar of two effects not overlapping with each other (for example, when indicating that frontal theta power was higher when accuracy was low compared to high). As the latter type of non-overlapping confidence interval is of greater interest in this study, these effects are depicted in plots as a darker grey shading for significant epochs (see Figure 4.2 as an example). For readers seeking to derive false-alarm-rate-controlled decisions from our analysis (i.e., via adjustments for multiple comparisons), it is noteworthy that the presented schema for highlighting consideration-worthy differences is conservative with respect to alpha. That is, at least for all differences involving within-subject comparisons, it is well-established that overlap of confidence intervals for means is typically larger than more rigorous inspection of the confidence interval for the difference between the means would reflect [71].

All scripts and details of the experimental software, preprocessing of behavioural and EEG data and final statistical analysis and plotting code are available online (https://github.com/LBRF/DEMI_Analysis_Pipeline).

4.3. RESULTS

Plots for all results described below are included in Appendix B, including effects of accuracy (high versus low; Appendix B Figure 1), effects for familiarity (repeated versus random; Appendix B Figure 2) and their interaction (plotted as low accuracy minus high accuracy [to depict error] for repeated versus random; Appendix B Figure 3) at each sensor location for each frequency band (theta, alpha, and beta) and group (overt and imagery). Selected results are plotted in the main text. Unless noted otherwise, only statistically significant results (or notable lack thereof) are discussed below.

4.3.1. Beta Band

In line with existing literature [27–29], relative to rest the OM group demonstrated a decrease in sensorimotor (e.g., C3 and surrounding sensors) beta power during movement followed by a relative increase after movement (the PMBS; Appendix B Figure 1). This change was most noticeable in the contralateral (to the hand performing the task) sensorimotor area (e.g., C3). Contrary to one of our hypotheses, the magnitude of the sensorimotor PMBS was not related to familiarity (Appendix B Figure 2), Notably, nor was it related to accuracy (Appendix B Figure 1), and while power returned closer to baseline it did not increase beyond this and demonstrate a typical PMBS response. Given previous results that suggest that the PMBS indexes confidence in the forward model and is suppressed by motor task error [28,29], our results may be due to the challenging nature of the task whereby considerable error is present throughout the experiment and in all conditions. Interestingly, there was an effect of accuracy in frontal and temporal sensors F7, FT7, and T7 both before and after movement (Appendix B Figure 1). There appeared to be no interaction between accuracy and familiarity in either group (Appendix B Figure 3).

Interestingly, for the MI group there were no apparent main effects of either accuracy or familiarity in the beta band (Appendix B Figure 1 and 2), except for a single sensor (Cz) where unfamiliar movements resulted in lower beta power. Thus, our hypothesis that imagery would not demonstrate a familiarity-related sensorimotor beta power increase (PMBS) was supported. However, we did observe in the MI group a significant decrease in beta power relative to rest both during and after movement that was most prominent in sensors overlying the contralateral premotor area (Appendix B Figure 1). Qualitatively, this beta decrease did not appear as strong as that observed in the OM group and was not accompanied by a relative increase after movement — that is, unlike the OM group, we did not observe evidence of PMBS in the MI group.

4.3.2. Alpha Band

For the OM group we observed significantly lower power in posterior parietal and occipital alpha power during low accuracy compared to high accuracy trials (Figure 4.2), which is in line with existing literature [26]. This effect was present both during and after movement, the latter result supporting our hypothesis that this would be observed. A single sensor (P7) demonstrated a significant interaction between accuracy and familiarity such that during familiar trials lower accuracy trials further decreased alpha power (Appendix B Figure 3). A significant main effect of familiarity was present such that unfamiliar trials resulted in lower alpha power in the occipital region and one frontal sensor (F4) during movement, and lower alpha power in the occipital and contralateral temporal regions after movement (Figure 4.3).

For the MI group we observed a significant interaction between accuracy and familiarity in the alpha band in two sensors (FC4 and C4) overlying the ipsilateral sensorimotor cortex (Appendix B Figure 1). Specifically, for unfamiliar (random pattern) trials compared to familiar (repeated pattern) trials, low accuracy was associated with decreased alpha power during the movement. Given that these effects were observed only for unfamiliar pattern low-accuracy trials, we suggest that this finding represents high uncertainty during these trials. With respect to main effects, the MI group did not demonstrate a decrease in power in the alpha frequency band over parietal and occipital regions related to accuracy (Figure 4.4), which is contrary to our hypothesis. Instead, MI demonstrated only two sensors sensitive to accuracy (F4 and CP3) during movement with differential effects (low accuracy significantly decreased alpha power in F4 while high accuracy significantly decreased alpha power in CP3). However, motor imagery demonstrated widespread significant unfamiliarity related (random movements) decreases in power in the alpha frequency band during movement (but not after) throughout central, ipsilateral parietal, and contralateral temporal and parietal regions (Figure 4.5). Overall, these observations suggest that during MI alpha power is related to familiarity (or movement uncertainty) in bilateral parietal regions, as opposed to during OM where alpha power is related to accuracy in posterior parietal and occipital regions.

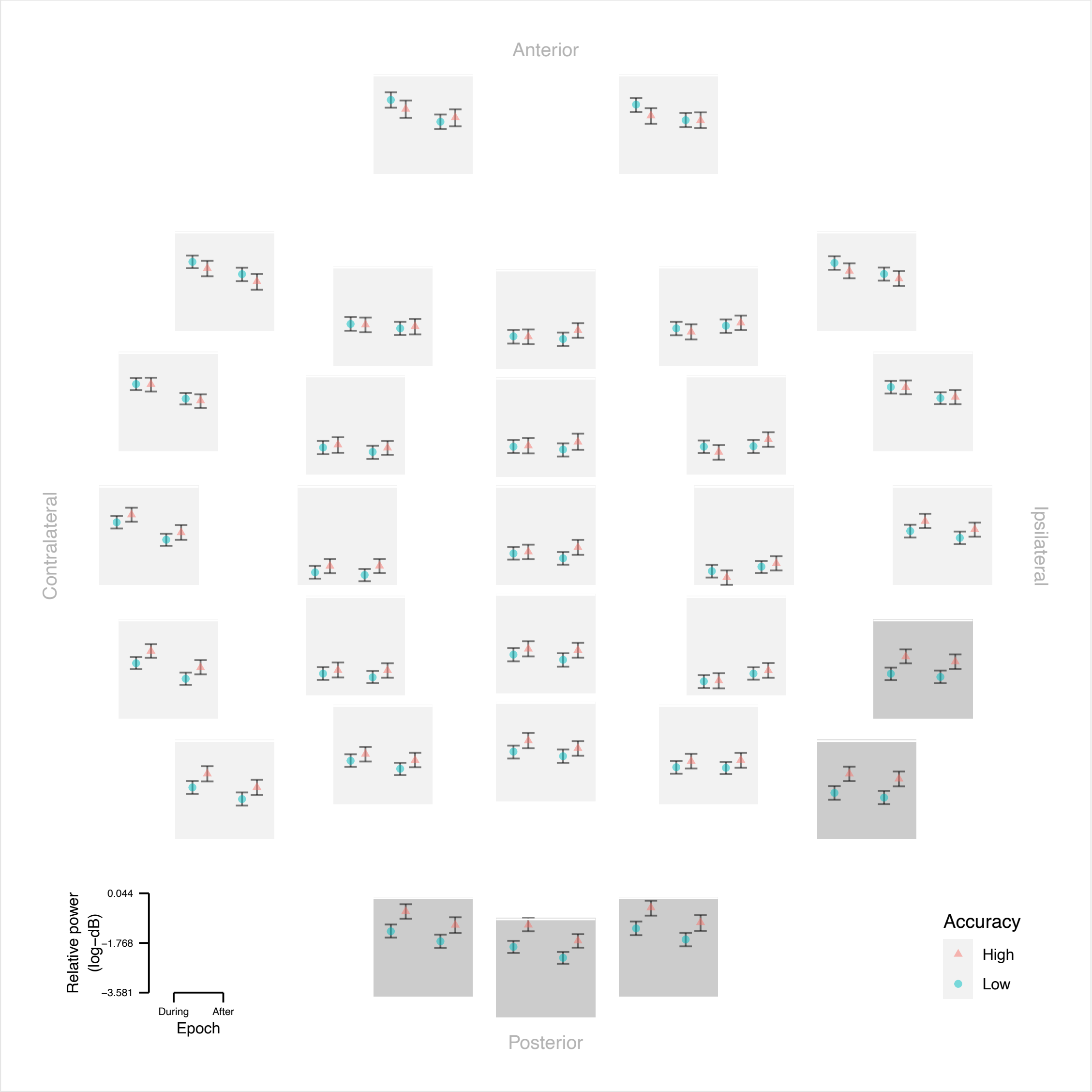

Figure 4.2. Accuracy related alpha power changes from baseline in the OM group, during and after movement, for each sensor. Contralateral here refers to the hemisphere opposite to the arm that performed the task. Epochs that demonstrated non-overlapping error bars between the factor of interest (in this case accuracy) are shaded darker for ease of interpretation. Where relevant in subsequent plots, a white line depicts zero on the y-axis. See legends for additional details.

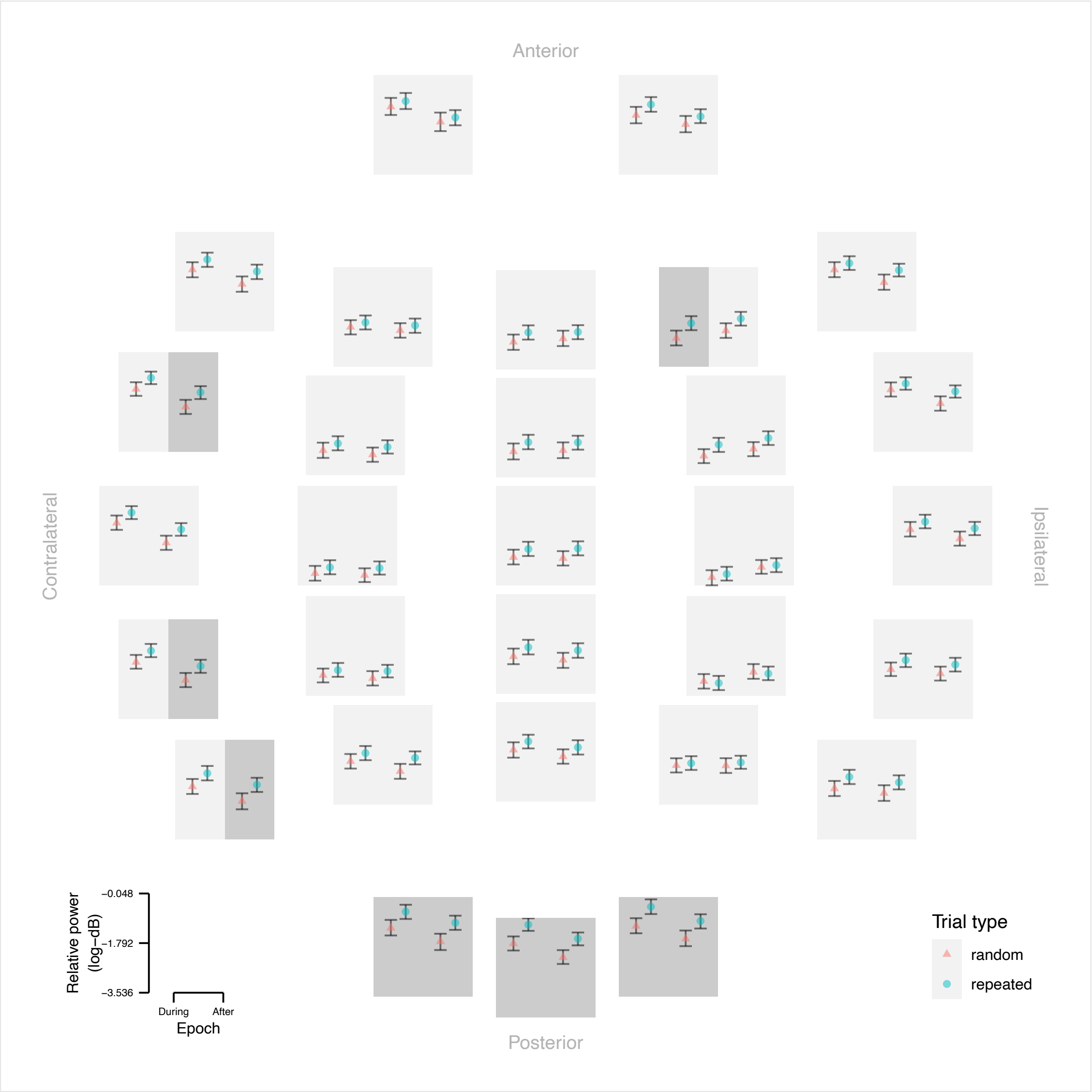

Figure 4.3. Familiarity (repeated versus random) related alpha power changes from baseline in the OM group, during and after movement, for each sensor.

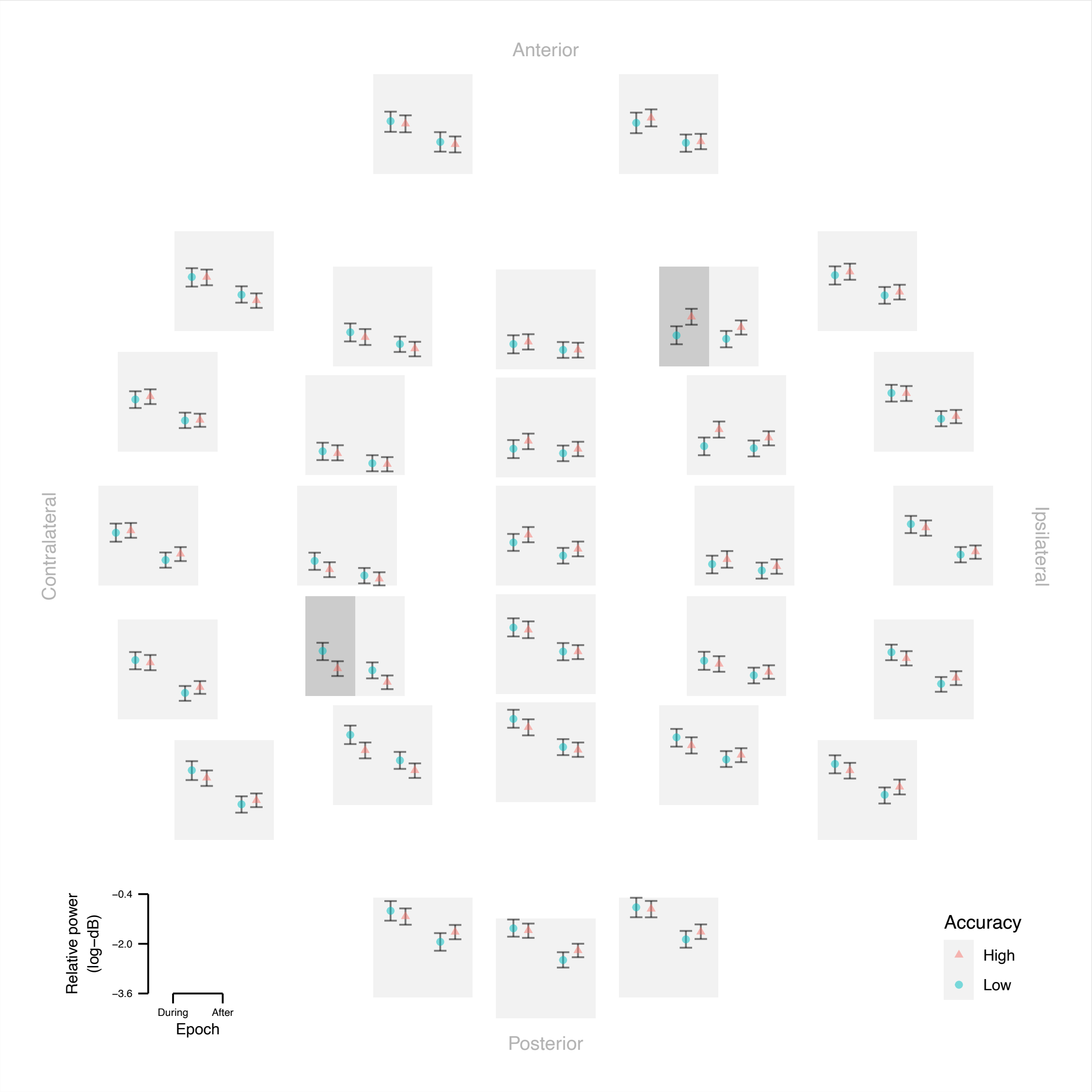

Figure 4.4. Accuracy related alpha power changes from baseline in the MI group, during and after movement, for each sensor.

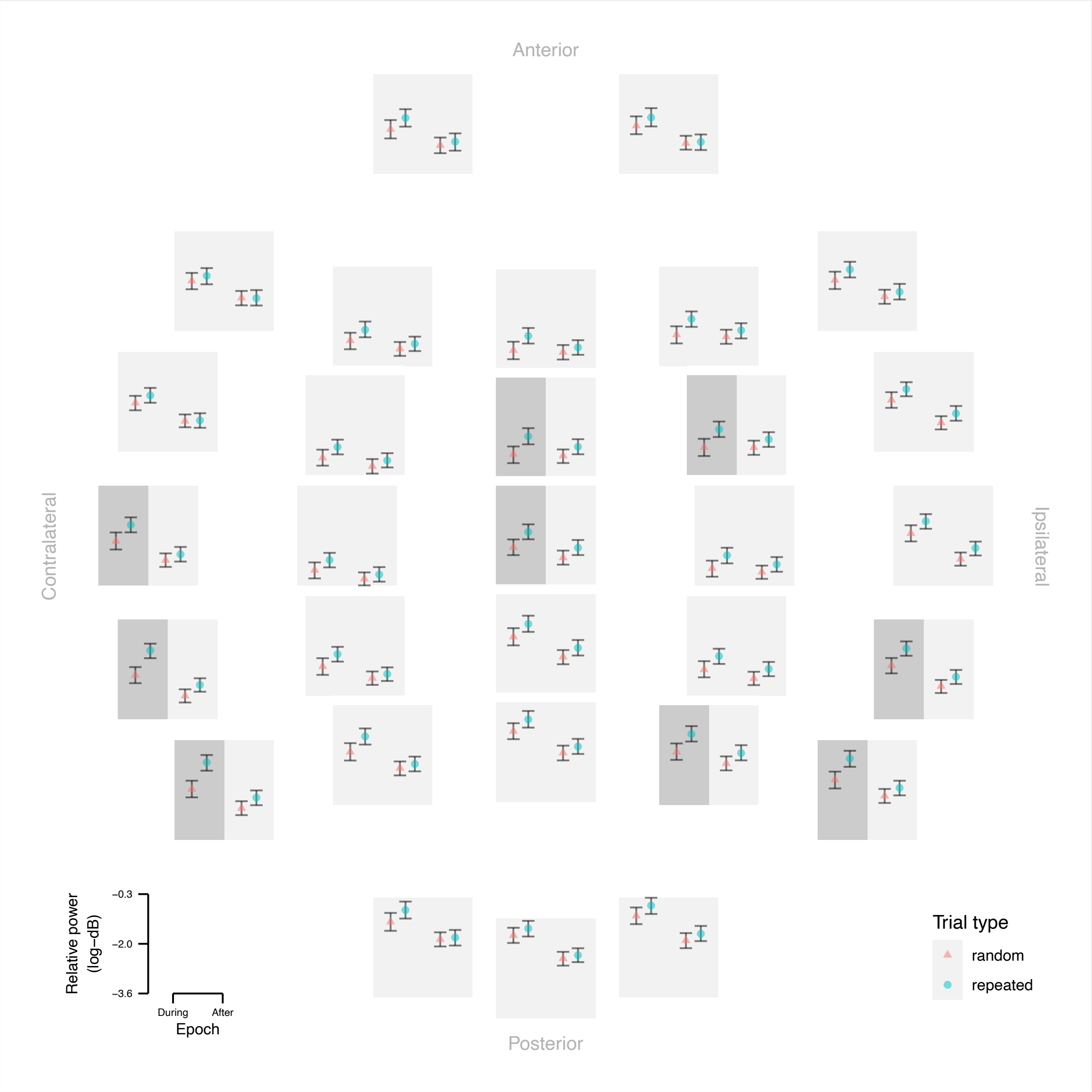

Figure 4.5. Familiarity related alpha power changes from baseline in the MI group, during and after movement, for each sensor.

4.3.4. Theta Band

For the OM group, we observed a significant increase in theta power over frontal regions during low accuracy movements compared to baseline, and in some sensors compared to high accuracy (Fp1 and F8; Figure 4.6), thus supporting our hypothesis. Error related increases in frontal theta power during motor tasks has been demonstrated previously [26]. The OM group also demonstrated a significant effect of familiarity where unfamiliar (random pattern) trials resulted in decreases in theta power during movement in the most lateral sensors of the frontal, temporal and parietal regions on the contralateral side, and after movement in contralateral central, parietal and temporal sensors (Figure 4.7). There was a significant interaction between accuracy and familiarity in a single parietal sensor (P7; see Appendix B Figure 3).

Interestingly, the IM group also demonstrated significant changes in frontal theta power during movement, except these changes were a decrease in theta power rather than an increase as observed in the OM group, and theta power was significantly lower during low accuracy trials than high accuracy trials (Figure 4.8). This does not support our hypothesis that MI would demonstrate similar frontal theta changes to OM but suggests a different role for frontal theta in imagery. Decreases in frontal theta power are associated with increased working memory load from the DLPFC [45], the implications of which will be elaborated upon in the discussion below. Unlike the OM group, the MI group did not demonstrate familiarity related changes in theta power (Appendix B Figure 2). However, the MI group did demonstrate a significant interaction of accuracy, familiarity, and epoch in the posterior parietal and occipital region whereby theta power decreased in familiar trials with low accuracy during but not after movement (Figure 4.9). The theta band changes related to low accuracy during familiar patterns is unlike the interaction observed in the alpha band which was related to low accuracy for unfamiliar trials (i.e., those featuring random trajectories). During familiar trials, participants should have a more accurate representation of the movement to imagine, and therefore low accuracy may in fact be related to the perception of error during motor imagery, a concept that is elaborated on in the discussion below.

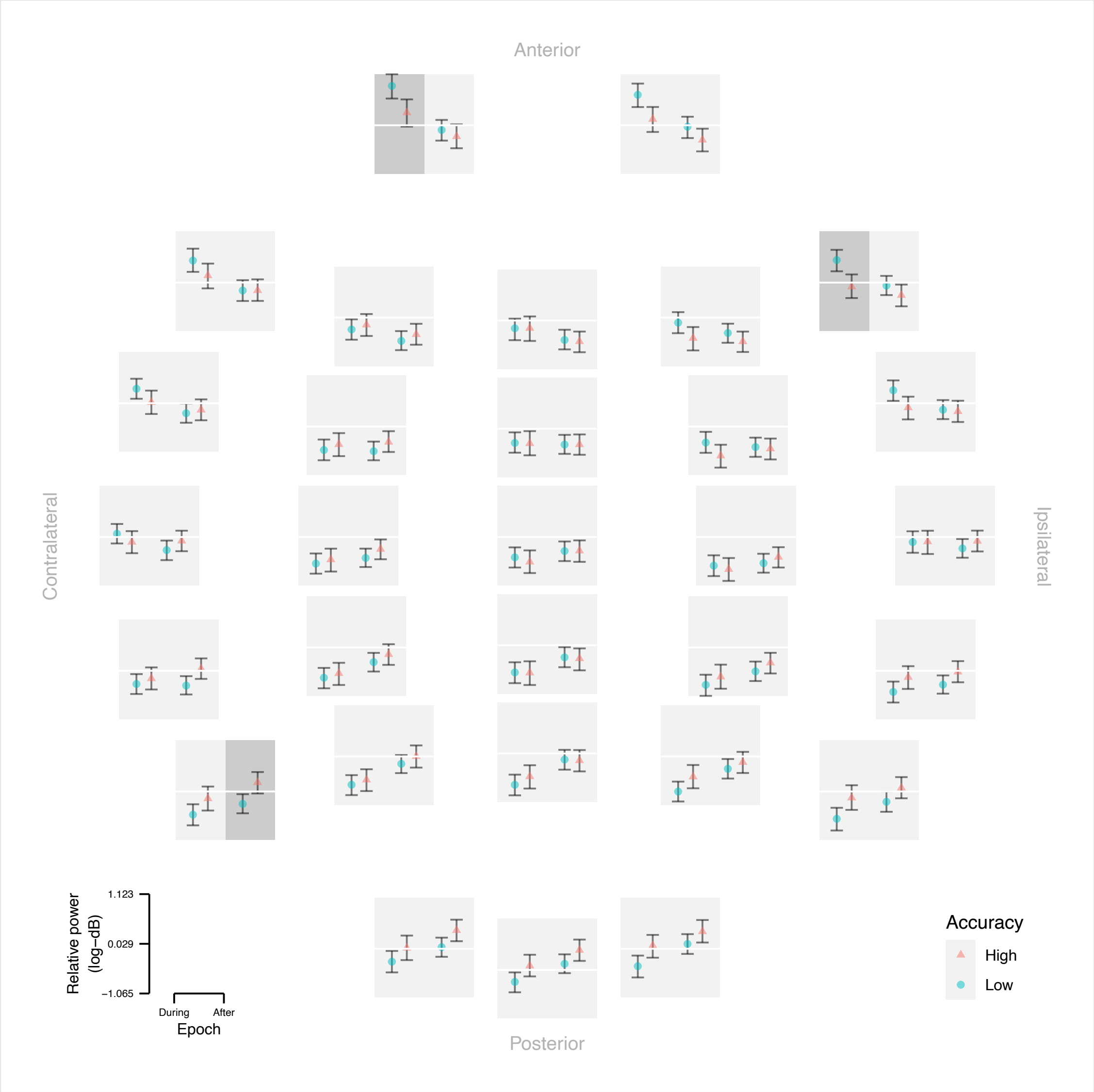

Figure 4.6. Accuracy related theta power changes from baseline in the OM group, during and after movement, for each sensor.

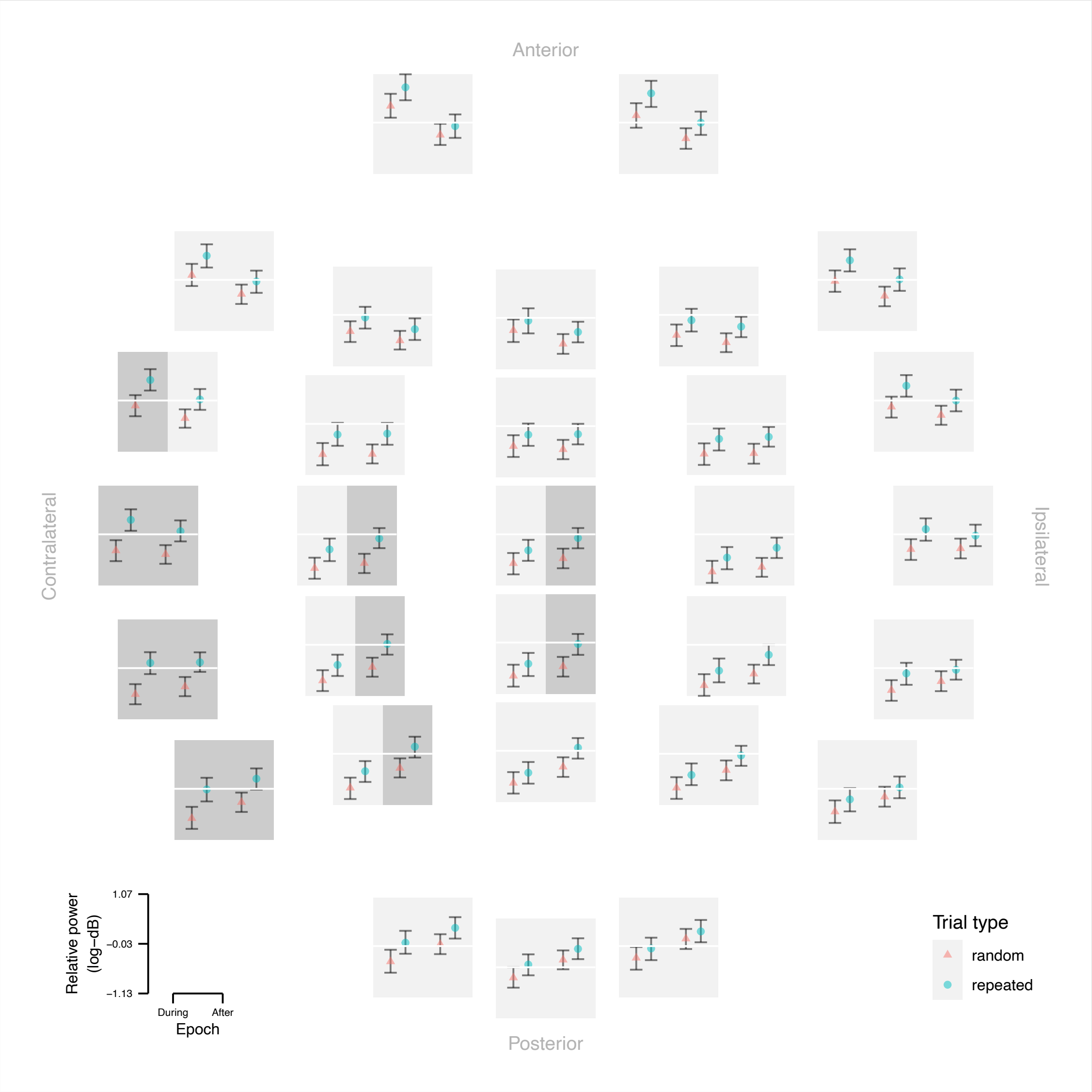

Figure 4.7. Familiarity related theta power changes from baseline in the OM group, during and after movement, for each sensor.

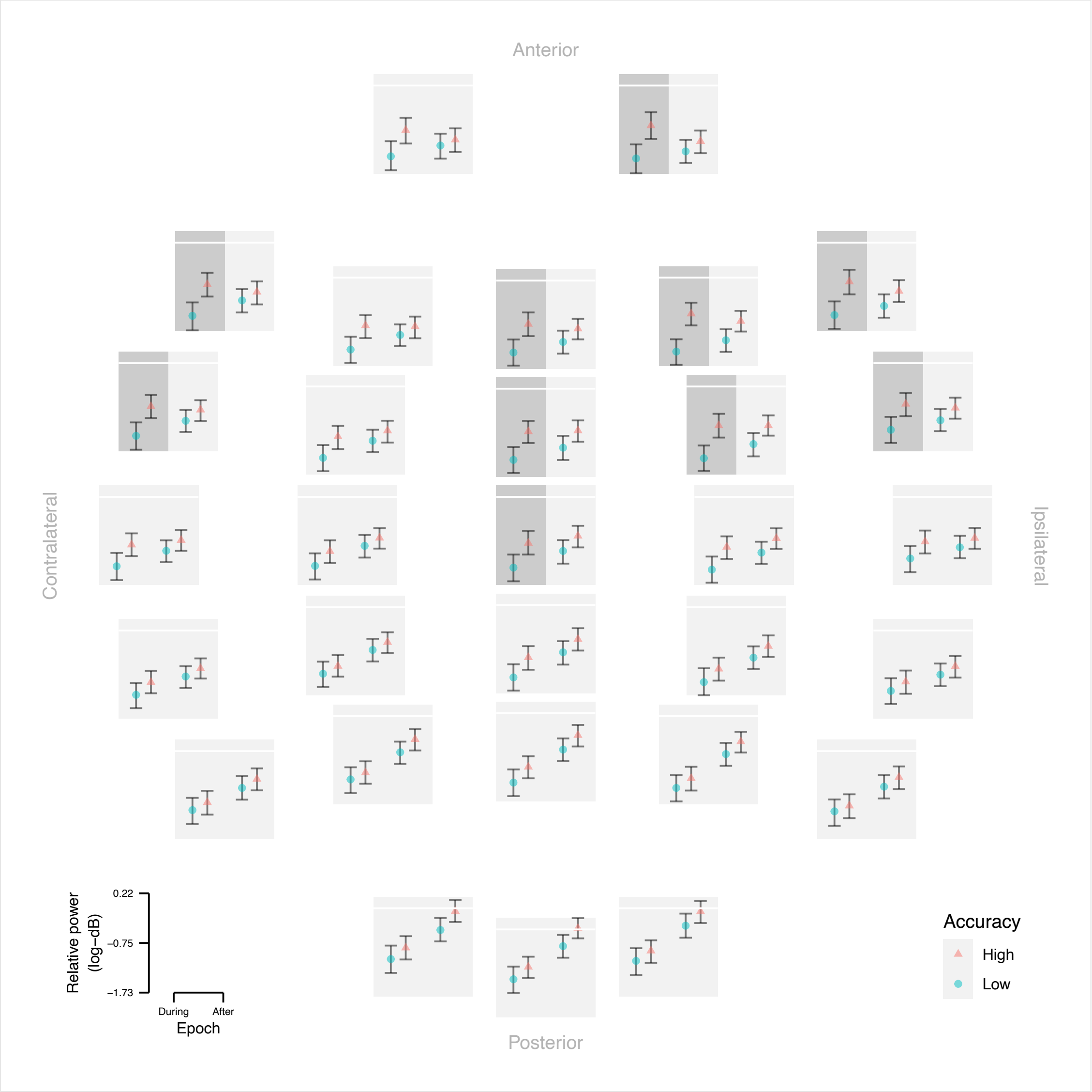

Figure 4.8. Accuracy related theta power changes from baseline in the MI group, during and after movement, for each sensor.

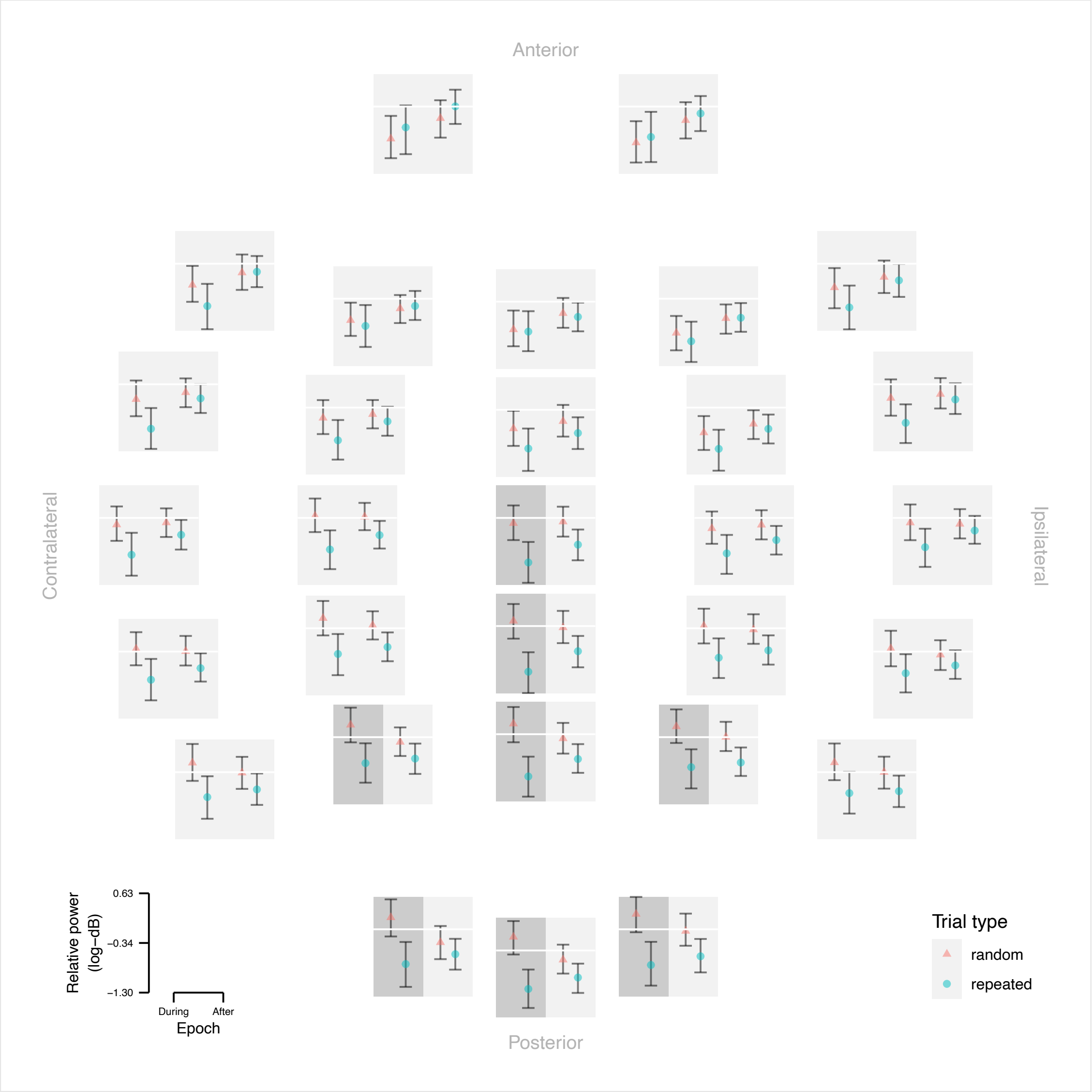

Figure 4.9. MI group interaction between familiarity and accuracy on theta power. Plot represents low accuracy minus high accuracy (error-related) theta power changes in either familiar (repeated) or unfamiliar (random) trials, during and after movement.

4.5. DISCUSSION

Our results offer evidence that movement accuracy is processed during motor imagery, but in substantially different ways compared to overt movement. Importantly, the results of our overt movement group replicate previous findings such as a decrease in movement-related sensorimotor beta power, post-movement sensorimotor beta power increases (the PMBS), error-related power increase in theta over mid frontal regions, and error-related power decrease over posterior parietal regions. We contribute to the existing literature by reporting accuracy and uncertainty related EEG power changes in motor imagery. Our MI group demonstrated negligible accuracy or uncertainty related effects in the beta band but did show uncertainty related changes during imagery in ipsilateral sensorimotor and bilateral parietal alpha power, and accuracy related changes in both frontal and parietal theta power. These findings, discussed in greater detail below, have important theoretical implications that may call for a reconciliation between competing theories of motor imagery.

Beta band power in the OM group demonstrated the expected movement-related power decrease with a relative post-movement power increase (the well-known PMBS) [27–29,46–48]. Interestingly, our results demonstrated that the PMBS was not related to familiarity (a proxy of uncertainty) of the movement pattern, or accuracy (a proxy of error). However, the post-movement increase never returned to baseline suggesting that PMBS may have been suppressed even during higher accuracy trials. Given existing evidence that the PMBS indexes a decreased weighting of sensory feedback and an increased weighting of confidence in the forward model rather than error [28,29], this may suggest that the task contained significant error throughout the experiment and confidence in a forward model was not reached. The MI group also demonstrated a more subtle but significant movement-related beta power decrease from baseline. Existing literature typically reports faint beta power decrease during motor imagery [32], but this may be related to the experimental tasks used. Our experimental task may have recruited contralateral sensorimotor beta processes to a greater degree given that the task is designed to challenge motor execution rather than upstream motor processes related to perception or planning [16,34,49]. Indeed, a previous report demonstrated that motor imagery of more challenging movements led to greater decrease in beta power in the contralateral sensorimotor cortex, and the authors attributed this to the computation of movement parameters [30]. It is important to note that we did not observe PMBS in the MI group. This may not be a surprising result given that the PMBS appears to be related to an assessment of sensory feedback as it relates to prediction error [29]. As will be discussed below, the absence of sensory feedback may force MI to utilize different processes to assess the quality of the imagined movement.

We found decreased alpha power in posterior parietal and occipital regions both during and after low-accuracy trials in the OM group, but not in the MI group. Error related decreases in alpha power over the PPC have been demonstrated to be related to errors driven by lapses in sustained attention during OM [26]. Conversely, the MI group demonstrated decreased alpha power during unfamiliar (i.e., random) movements in sensors overlying the ipsilateral sensorimotor and bilateral parietal regions, with a significant interaction between accuracy and familiarity. That is, unfamiliar trials with low accuracy demonstrated decreases in sensorimotor alpha power. This accuracy-related finding is interesting given previously reported findings that sensorimotor alpha power typically decreases during motor tasks but increases when task demands require greater action selection, potentially driven by inhibition of task-irrelevant cortical regions [30]. We observed a decrease in sensorimotor alpha power in the most challenging imagery trials (unfamiliar trials that resulted in low accuracy ratings), which may be a result of uncertainty — that is, the motor system was unable to adequately process the task demands. Indeed, a previous finding in infants has demonstrated decreased alpha power when observing unusual versus ordinary movements [50], and the parietal cortex is implicated in motor task attention [51–54]. Anecdotally, participants in the present study often remarked that during trials that featured more difficult randomly generated patterns, they were not sure how to respond. Curiously, this effect was not observed in the OM group, suggesting that during overtly executed trials participants may have decided to respond with largely arbitrary movements, while MI participants made no such decision and may have continued grappling with the motor plan during imagery, leading to an extended search for movement strategies as though action selection was not finalized when movement began. Therefore, we interpret our alpha band results in the MI group as resulting from the processing of motor task uncertainty.

Interestingly, both OM and MI resulted in accuracy related changes in frontal theta, but in opposite directions. Specifically, we observed increases in frontal theta power during overt movement in low accuracy trials but decreased frontal theta power during motor imagery in low accuracy trials. We propose that decreased frontal theta power during imagery may arise from DLPFC processing related to the increased working memory demands during more challenging bouts of imagery, in line with one of the predictions of the motor-cognitive model of motor imagery [6,55]. Typically, studies using sensor-level EEG report an increase in frontal theta power that may represent a realization for the need for cognitive control, which would occur in the presence of novel information, conflicting information, or the detection of error [56–58]. Importantly, increased frontal theta power has been largely attributed to volume conduction from deeper brain areas such as the anterior cingulate cortex and hippocampus [45,56]. While increased working memory demands have also been demonstrated to be associated with increased frontal theta power [59], and motor imagery has been shown to result in greater frontal theta power [60], we contend that these results may be due to volume conduction from deeper structures. Indeed, more direct measurements of DLPFC appear to reveal a decrease in theta power related to increased working memory demands [45], and motor imagery has been demonstrated to more consistently activate DLPFC compared to overt movement in fMRI studies [8]. Given our use of current source density to reduce the effects of volume conduction, we suggest that our analysis revealed a dissociation between OM and MI — that is, that the low-accuracy related frontal theta power increases observed in the OM group represent error processing, while the low-accuracy related frontal theta power decreases observed in the MI group represent greater executive demands associated with imagining more difficult movements.

While our results suggest that theta power changes over frontal regions appear to have a different role during imagery compared to overt movement, this should not be taken as evidence that motor imagery does not involve error processing. On the contrary, the MI group demonstrated a significant interaction between accuracy and familiarity in the posterior parietal and occipital region during imagery. That is, theta power over the PPC decreased when accuracy was low on familiar trials during motor imagery, but not after. Given that on familiar trials participants likely had developed a representation of the movement pattern to be imagined, we propose that low accuracy may be the result of a poorly performed motor simulation — an error during motor imagery. Given that PPC theta power increases have been associated with feedforward visuomotor prediction error processing [61,62], we propose that the increased PPC activation typically observed during motor imagery is due to an assessment of the predicted sensorimotor consequences compared to the desired consequences. Indeed, the parietal cortex has been implicated in anticipating movement dynamics via forward modelling [63–65].

Overall, our findings demonstrate neurophysiological evidence that movement accuracy is processed during motor imagery, but in considerably different ways than OM. In fact, while we replicate the finding that MI and OM utilize similar brain regions, our analysis of the processing occurring at each region found no similarities with respect to movement accuracy and movement familiarity related processing as evidenced by changes in power across multiple frequency bands. As such, our results conflict with the notion of functional equivalence. We provide evidence in favor of a key prediction of the Motor-Cognitive model: that imagery involves greater cognitive resources and executive processing. However, our results do not necessarily align with another prediction of the Motor-Cognitive model: that motor imagery doesn't involve the motor system upon the execution stage. Instead, we suggest that while motor imagery is a fundamentally different process from overt movement, imagery does recruit established components of the motor system but utilizes this system differently. Motor imagery appears to involve the forward modelling process and neural regions that implement them such as the parietal cortex, and in fact has a greater reliance on them. This reliance is evidenced by literature demonstrating that patients with parietal lobe damage are impaired in their ability to perform motor imagery [66–68], and motor learning via motor imagery is disrupted with inhibitory brain stimulation to areas of the parietal cortex but not motor cortex [69,70]. We suggest that this greater reliance on parietal regions support the notion of a motor simulation during imagery — that is, motor imagery compensates for a lack of sensory information by performing a simulation of the movement to predict its sensory consequences, enabling a comparison with the intended sensory consequences. Performing this simulation requires considerable cognitive effort which may be exhausted by greater task complexity and interference tasks [6,55]. Even so, motor imagery-based simulation recruits key regions throughout the motor system to estimate movement parameters and their potential outcomes. In conclusion, motor imagery utilizes the existing motor system but asks it to perform a task that it is not primarily designed to do, which requires cognitive effort. Importantly, our analysis was largely exploratory and correlational in nature and should not be interpreted as confirmatory. We hope our findings contribute to future work involving more targeted investigations with experimental designs that may speak to causal mechanisms underlying motor imagery.

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CHAPTER 5 | GENERAL DISCUSSION

5.0. PURPOSE OF EXPERIMENTS

The overall purpose of the experiments reported in this dissertation was to investigate whether motor imagery can be used to learn a novel movement skill, and how that might be possible. Importantly, these studies were meant to differ from previous studies that have employed experimental tasks where improvements may have been due to processes other than improvements in movement execution. That is, it is possible that motor imagery can improve goal selection (e.g., deciding what to do based on perceptual and cognitive processes), action selection (e.g., better mapping of movements or sequences of movements to the desired outcomes, or better movement planning), but cannot improve the execution of the movement itself. To answer this question a new experimental task was developed to challenge the movement execution, and learning was operationalized as a change in the speed accuracy function — that is, participants only demonstrated learning if they were able to perform with less error at the same speed, the same error at faster speeds, or both. The first experiment investigated whether motor imagery-based practice could drive learning in this task over and above a perceptual control group, and how the magnitude of learning compared to physical practice. Given that learning is typically driven by a comparative mechanism — that is, comparing intended and expected performance to actual performance as indicated by sensory feedback, which then provides a measure of error that provides a basis for refining future attempts — the second experiment investigated whether the quality of action execution was perceptible during motor imagery. This was done by investigating whether known drivers of execution performance similarly modulated participants self-reported accuracy ratings during imagery. Finally, the third experiment investigated whether these self-reported accuracy ratings are involved in a comparative mechanism by seeking their neurophysiological correlates — that is, whether neurophysiological measures correlate with accuracy ratings during motor imagery, which would imply that this information is being processed — and whether these correlates were similar (e.g., by anatomical location) to those observed during overt movement. Here I report the findings of these experiments, followed by a discussion of how these findings inform the existing literature on motor imagery and motor learning.

5.1. SUMMARY OF FINDINGS BY CHAPTER

Chapter 2 – Movement Related Sensory Feedback is Not Necessary for Learning to Execute a Motor Skill.[1] After five days of motor imagery-based practice, participants were able to learn to better execute a novel motor skill. That is, the speed accuracy function shifted in the direction of better performance on the specific movement pattern they were tasked with learning compared to randomly generated movement patterns of similar complexity. Importantly, motor learning was not observed in a perceptual control task that involved attending to the movement patterns without replicating the movement via motor imagery or physical practice. Interestingly, unless additional visual feedback of results were available, the physical practice group also did not demonstrate learning — indicating that physical practice may include an expectation of sensory feedback and ultimately depend on it. This might suggest that during the execution phase motor imagery relies entirely on predicted sensory feedback and is therefore not disrupted by a lack of actual sensory feedback. However, when feedback of results is available during physical practice, the learning effect is large, exceeding that of motor imagery after several days of practice. Overall, these results suggest that while physical practice with sensory feedback is more effective, motor imagery is capable of driving motor skill learning. Specifically, this study demonstrates for the first time that motor imagery can improve action execution of a complex motor skill. These results and those of others — notably Kilteni et al. (2018) demonstrating the involvement of forward models in motor imagery [2] — prompted questions about whether this finding implied that motor imagery-based learning involved a comparative mechanism; that is, that motor imagery may involve comparing predicted outcomes to intended outcomes rather than predicted outcomes to actual outcomes, deriving an error signal upon which to base learning.

Chapter 3 – Imagined Movement Accuracy is Strongly Associated with Drivers of Overt Movement Error and Weakly Associated with Imagery Vividness. Given that it is impossible to assess task error during motor imagery given that performance is entirely covert, this experiment aimed to investigate whether a proxy measure — that is, self-reported accuracy of imagined movements — was modulated by known drivers of error, such as speed, complexity, and familiarity (practice time). A physical practice group who also self-reported their performance accuracy was used to develop a model relating these drivers of performance with actual error. This allowed for a model that predicted an expected error from a trial given its speed, complexity, familiarity (the repeated vs. random movements) and experience (trial number). This model was then used to compute expected error during imagery trials so that it could be correlated with self-rated accuracy. The results demonstrated that self-ratings of accuracy were indeed well correlated with expected error, and that this was true in both imagery and physical conditions. Furthermore, these self-reported accuracy ratings improved with experience in a similar way as seen during physical practice. Finally, kinematic complexity of the movement did not differently affect motor imagery participants ability to match movement times compared to overt movement participants. This latter result differs from previous studies that demonstrate that increasing task complexity disrupts motor imagery movement times [3] — however we contend in the discussion of Chapter 3 that this is due to the nature of the experimental tasks used, and that this effect is a function of cognitive interference in previous experiments. Taken together, the results of this study demonstrate that motor imagery appears to involve task performance — not simply task planning — as evidenced by self-reported sensitivity to drivers of error like speed, complexity, and experience. Overall, these results provide evidence that motor imagery involves the processing of imagined movement accuracy, which may serve as a basis for a comparative mechanism that drives motor learning.

Chapter 4 – Neurophysiological Correlates of Accuracy During and After Imagined Movement Execution. The final experiment added to the previous findings by investigating the neurophysiological correlates of self-reported accuracy as well as familiarity (e.g., repeated versus random movements) using electroencephalography (EEG) in both overt and imagined movement. As expected, given the existing literature, overt movement demonstrated a movement-related sensorimotor beta power decrease, a post movement sensorimotor beta power increase (the PMBS), error (in this case, low accuracy) related frontal theta power increase, and error-related posterior parietal power decrease. However, these neurophysiological patterns differed markedly in the motor imagery condition. For motor imagery there were negligible accuracy or familiarity related differences in the beta frequency range, but there was an unfamiliarity (or uncertainty) related alpha power decrease during imagery in the ipsilateral sensorimotor and bilateral parietal regions, error (low accuracy) related theta power decrease during imagery in the frontal region, and an interaction whereby familiar movements led to error (low accuracy) related theta power decrease during imagery in the posterior parietal and occipital cortex. Taken together these results provide evidence that the accuracy of imagined movements is indeed processed during imagery, implying that comparative mechanisms may exist during motor imagery. These results also provide support for certain aspects or interpretations of both motor simulation theory and the motor-cognitive model, which will be discussed below.

5.2. THEORIES OF MOTOR IMAGERY

Prominent theories of motor imagery appear to differ from one another primarily in their emphasis of the *importance* of cognitive processing or the *involvement* of the motor system. For instance, the motor-cognitive model suggests that the motor system is not engaged and that while motor imagery involves the same planning stages as overt movement, the execution of an imagined movement is handled by executive functions that rely on cognitive resources [3]. Cognitive models also tend to emphasize the need for an existing (i.e., previously experienced) movement representation to aid or even enable motor imagery [3,4]. Motor simulation [5] (or emulation [6]) theories suppose that motor imagery does involve the motor system — so much so that they hypothesize that neural activation during imagery is functionally equivalent to that of overt movement, and that cognitive processing (e.g., via frontal cortical regions) are mostly involved in the inhibition of overt movement [7]. While authors who espouse either of these theories can point to empirical support, there also exists conflicting evidence for each perspective as reviewed in detail in Chapter 1 (particularly sections 1.5.1 and 1.5.2). For instance, there is compelling evidence for forward modelling during motor imagery [2], a process that is considered fundamental to the control of overt movement [8–13], which therefore implies involvement of the motor system during motor imagery. But while motor imagery appears to involve the motor system, it is also more sensitive to cognitive interference than overt movement [3], and the outcomes of imagery-based practice differ from physical practice with respect to the content, timing, and magnitude of learning [14–17]. Indeed, a recent neuroimaging meta-analysis demonstrated that motor imagery does more consistently involve activation in brain regions associated with cognitive processing (e.g., pre-frontal cortex) but also demonstrates consistent activation in regions associated with movement (e.g., premotor cortex, parietal cortex, and cerebellum) [18]. Overall, it appears that these theories are neither completely correct nor incorrect and will be superseded by a theory of motor imagery that integrates aspects of each.

The experimental findings presented in this dissertation may aid in the development of an updated model of motor imagery, and example of which will be described here and is depicted in Figure 5.1 below. I hypothesize that motor imagery involves a simulation of the intended movement and that the processing involved in coming to this movement intention is largely the same as it would be for overt movement, except for the important difference that there is awareness that the movement will not be overtly performed. The results from Chapter 2 support this notion given that a lack of sensory feedback appeared to disrupt learning via overt practice but not imagery-based practice, which implies that feedback is expected and perhaps necessary for motor learning during overt practice but not imagery-based practice, where sensory feedback is not expected. In this model, the intended movement represents the desired outcomes (e.g., the desired state change, such as moving the body closer to a reward given the environmental context; involving parietal regions [19,20]), and simulation refers to the covert unfolding of the movement using the existing computational resources of the motor system: that is, a feedback control policy (e.g., involving premotor and potentially primary motor regions — but with descending motor commands suppressed), an efference copy, the forward model (e.g., involving the cerebellum), sensory consequence prediction, and state estimation with a comparative mechanism (e.g., involving parietal regions again) which feed into the feedback controller. This process loops until the movement is complete and given that the movement does not result in an effector reaching a new position in the environment, the evolving state estimation process operates as a simulation that may contrast with reality — ignoring reality and allowing simulation likely requires cognitive effort. This is supported by Chapter 4 demonstrating that processing in parietal regions during imagery differ from that observed during overt execution but are still associated with the quality of the imagined movement. Critically, motor imagery involves a greater emphasis of the intended movement consequences to the state estimator (e.g., parietal cortex) given the lack of sensory feedback, allowing a comparison between predicted movement outcomes with intended movement outcomes. This is supported by both Chapter 3 and 4, where the former supports the existence of an assessment of imagined movement accuracy and the latter demonstrates that it is associated with frontal and parietal cortical processing that differs from overt movement. It is the state estimation resulting from this comparison that is fed to the feedback controller, which is less detailed than that provided by actual sensory feedback. This is supported by Chapters 2 and 3, where the former demonstrates that the magnitude of learning via imagery-based practice is less than overt practice, and the latter demonstrates that self-reported accuracy is generally higher during imagery than for overt movement when actual sensory feedback is available. As such, while motor imagery involves the use of the motor system, the underlying computations are likely different in important ways that should be explored in future research. Furthermore, given that upstream cognitive processing is required to engage the motor system in simulation — including an instruction to imagine and possible motor inhibition — motor imagery is readily disrupted by cognitive interference as suggested by the motor-cognitive model [3]. A key feature of the novel model presented here is that it aligns well with existing motor control theories that recognize the problem of motor redundancy (or motor equivalence) where the motor system can achieve a given goal in a near-infinite number of ways [21,22], which implies that the storage of specific movement representations is not reasonable. Instead, the motor system establishes a goal and flexibly achieves it via optimal control [13,23,24]. Given that motor imagery utilizes these computational resources, it should be capable of forming novel movement representations — such as changes in a control policy or forward model — and imagery-based practice should be capable of novel motor skill learning (as described in section 1.2.2). This is supported in Chapter 2 where imagery-based practice led to novel motor skill learning. The role of motor imagery in motor learning will be further explored below (section 5.3).

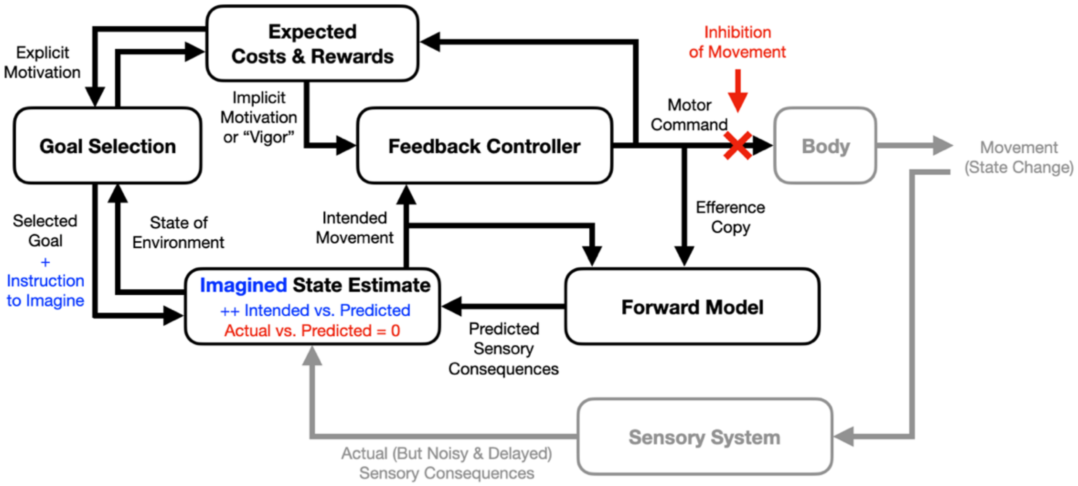

Figure 5.1. Proposed Computational Model of Motor Imagery.

This novel model of motor imagery has desirable strengths but is limited by its focus on how motor imagery handles action execution. Indeed, the purpose of this dissertation (stated in section 1.6) was to investigate whether motor imagery is capable of driving motor skill learning (section 1.2.2), with an explicit focus on action execution rather than action selection (section 1.2.3), and how this might occur. This involved designing an experimental task specific to this purpose and as such the results of the experiments presented within must be interpreted within the broader literature. The model of motor imagery presented above speaks specifically to the online processing that occurs during an imagined movement but speaks very little to upstream processes — such as perception, motivation, decision-making, movement planning, and more — that are critical for a complete understanding of motor imagery [14,17,25–27]. Indeed, even the most prominent and prolific proponents of computational perspectives of motor control and learning have begun turning their attention to decision-making and cognitive processing [28,29], which is further attestation for the importance of understanding upstream processes.

Furthermore, the model described above speaks little to processes that occur at different timescales, such as hours or days after an imagined movement — where for example mental practice has been shown to reveal differences in the content and magnitude of motor skill consolidation compared to physical practice [16,17]. Despite these limitations, the experiments presented above represent novel and important contributions to the motor imagery literature and may inform the development of new models of motor imagery including the model proposed above. Specifically, the proposed model provides a basis upon which motor skill learning — specifically improvements in action execution — may be capable via motor imagery.

5.3. MOTOR LEARNING VIA MOTOR IMAGERY

The results of the experiments presented in this dissertation and existing literature suggest that it is indeed possible to improve the quality of a movement without overtly executing it. The emphasis on action execution rather than upstream processes like goal selection or action selection is important given that motor imagery has long been thought to share the same motor planning processes as overt movement but diverge at the execution stage. This implies that motor imagery can drive motor learning via improvements to these upstream processes but does not imply that imagery can drive improvements in action execution. For instance, it has been demonstrated that motor imagery is capable of driving performance improvement in both adaptation and motor sequence learning tasks [15,16,30,31]. What's more, in the case of a keyboard sequence task, it appears that learning via motor imagery is readily disrupted by the alteration of a sensory cue as opposed to a switch of the hand performing the task, and the inverse is true for physical practice-based learning [25]. This suggests that motor imagery-based learning is more reliant on perceptual processing and is not dependent on the effector performing the task. However, sequence tasks are implicated in challenging action selection processes [32,33], rather than action execution. Similarly, during adaptation tasks that involve a predictable perturbation in a simple reaching movement, participants can reduce error by simply aiming in a different direction to compensate for the perturbation which can be seen as primarily an action selection challenge rather than an action execution challenge per se [34–36]. If one adopts the view that motor imagery is primarily a perceptual, cognitive, or motor planning process, then it may not be surprising that motor imagery is capable of driving improvement in these tasks given their demands. Whether imagery can be utilized to drive improvement in the quality of an executed action remains questionable in this view. However, the results presented in this dissertation — particularly chapter 2 — suggest that motor imagery is indeed capable of driving improvements in action execution.

The mechanisms of imagery-based motor skill learning can be hypothesized in the context of the motor imagery model presented in Figure 5.1. During motor imagery the intended movement is simulated using the computational resources of the feedback controller, forward model, and state estimator, the latter of which relies on a comparison between the intended movement consequences and the predicted movement consequences. As such, both the feedback controller and forward models are afforded with information necessary to drive updates. This is supported by recent evidence demonstrating that motor imagery involves the use of a forward model to predict sensory consequences of an imagined movement [2]. As discussed in section 1.5.3, further support can be found in recent studies of covert movement in animals (using brain-computer interfaces implanted in pre-motor and primary motor cortices) and motor imagery in humans (using an adaptation task) that together suggest that imagery can set the initial state of a movement [31,37] — a key concept in modern theories of motor cortex function (described in section 1.4.3) [38,39]. Therefore, motor imagery may drive input to the premotor and primary motor cortex that contribute to the development of novel combinations of motor primitives (see section 1.4.3) to construct complex but discrete motor plans (see section 1.3.4) or motor programs (see section 1.3.1) and then simulate whether they may be successful to drive further refinement. These refinements may occur in motor and parietal cortical regions, as well as cerebellum given that forward models may be subject to refinement as well. Critical to this updating process is a comparative mechanism that relies on parietal cortex, which may extend broadly to motor learning via mental practice in a wide variety of tasks. Indeed, damage to the parietal cortex impairs motor imagery ability [40] and inhibitory brain stimulation to the parietal cortex can disrupt sequence learning [26]. Note that inhibitory brain stimulation to the primary motor cortex does not disrupt sequence learning via imagery [41] — but primary motor cortex (along with premotor cortex and cerebellum) has been demonstrated to be critical for motor skill learning of action execution in physical practice [42]. Therefore, inhibitory brain stimulation to the premotor and primary motor cortices during tasks that emphasize action execution rather than action selection, and observing the effects on motor skill learning, would therefore represent a critical test of the motor imagery model presented here.

What is learned via motor imagery is likely a function of three factors: training time, task demands, and the nature of motor imagery. The model above suggests that motor imagery has inherent limitations — particularly the reliance on motor simulation and the lack of precision feedback afforded by the sensory system. While Chapter 2 demonstrates that with enough time substantial motor skill learning can occur via mental practice, physical practice drives a greater magnitude of learning. It is possible that the difference between the two training methods would only widen as expertise increases, as refinements in action execution are likely subtle and will rely more on fine detail. However, it is also possible that when combined with physical practice, motor imagery is capable of more detailed simulation. Indeed, it has been shown that experience does modulate motor imagery in a similar manner as physical practice [43]. It has already been discussed how task demands will modulate the content of imagery-based motor learning, but it is worth highlighting that the motor imagery model described above does not speak to differences between so-called effector dependent or effector independent information. Broadly, effector dependent information refers to details of a movement that are specific to the part of the body performing the movement (e.g., left hand muscle activation) while effector independent information refers to movement related details that are independent of the body part performing the movement (e.g., features of the goal, including the shape of the movement — for instance, writing your signature with your foot). The motor imagery model above implies that both types of information are likely involved in action execution, and therefore it may be difficult to dissociate the two when performing imagery experiments on tasks that emphasize action execution over action selection. However, this would represent an interesting research program detailing how imagery is capable of driving motor skill learning of action execution.

5.4. LIMITATIONS, OPEN QUESTIONS AND FUTURE DIRECTIONS

Conclusions drawn from the findings presented here should be interpreted considering the limitations of the experiments. All three experiments utilized a novel experimental task with no previously published results upon which to base experimental design considerations, such as a power analysis — a common issue in neuroscience [44,45]. This was mitigated to some degree by doubling sample sizes typically reported in neuroimaging and cognitive neuroscience literature (typical being N=30 [45], but Chapter 2 had N=60, Chapter 3 and 4 N=80). Furthermore, in all three experiments hierarchical models were utilized to characterize and account for more sources of variability than simply averaging trials to produce a single performance variable per participant, which has been shown to improve generalizability of results [46]. Indeed, performance variability was high in the experimental task used (see the first figure of Chapter 1 for a depiction of this variability), which is not surprising given its complexity. The findings of each study are limited in scope by the experimental task used — a point repeated throughout this dissertation but no less a limitation of the experiments presented within. Also common between each experiment is the conceptual challenge of mapping objective measures to cognitive processes theorized to exist and designing experiments to isolate them. While these processes are described in serial (e.g., representational model, Figure 1.2) and with limited relationships between them (e.g., computational models, Figure 1.1 and Figure 5.1) to facilitate interpretability of the literature and results, these processes likely occur largely in parallel and with more interdependence than described. Another conceptual challenge present in any study of motor imagery is a lack of measurable behaviours due to its covert nature, which is a particular challenge for Chapters 3 and 4. That is, the self-reported accuracy rating is clearly an imperfect representation of the accuracy of an imagined movement. This is clear given the result reported in Chapter 2 that actual error (measured in the overt movement group) only accounted for about half the variance observe in self-reported accuracy.

It remains to be seen whether the motor imagery model presented in this general discussion is accepted by other motor imagery researchers and tested or elaborated upon with new experiments. In any case, there are several interesting questions raised by the model that can be investigated with well designed experiments. For example, the model poses a more specific role for the primary motor cortex in driving motor skill learning for tasks that emphasize and measure the quality of action execution. This possibility is readily testable with inhibitory brain stimulation to the primary motor cortex. If null results are found, the experiment should be replicated with premotor cortex before the model is completely jettisoned. This is because it's possible the primary motor cortex is not involved during imagery and the concept of setting an initial state for a movement can be achieved in the premotor cortex. The model also proposes more detailed roles for the frontal and parietal cortices during motor imagery. That is, the frontal cortex may be involved in both inhibition of a descending motor command — which again may be tested with inhibitory brain stimulation — and potentially a role in instructing the parietal cortex in performing a comparison between the intended movement and the results of a simulated movement. How the frontal cortex influences this comparative process remains an open question. Literature suggests that an intended movement originates from the posterior parietal cortex, specifically the inferior parietal lobule [47] — suggesting that the parietal cortex is involved in estimating the sensory consequences of an imagined movement (with input from a cerebellar forward model), producing an intended movement from the desired consequences, and comparing the intended consequences from the simulated consequences. This suggests a high degree of processing in the parietal cortex during motor imagery, potentially in several different subregions that interact as a complex network. A thorough understanding of how the parietal cortex is involved in motor imagery appears critical and likely requires multiple research programs using a variety of experimental approaches. Finally, it is necessary to understand how the model described here fits within a more comprehensive understanding of motor imagery, including different tasks, processes (e.g., including goal and action selection) and timescales of learning.

Finally, the results and discussion here highlight the importance of considering experimental design in applied motor imagery research. For instance, studies investigating the utility of motor imagery in sports should consider carefully the skill being investigated, whether a motor or cognitive skill critical to success. The findings reported here suggest that the execution of complex movements are capable of being learned and subsequently improved upon via motor imagery. The author once interviewed a pole vault athlete that reported that their training frequently involved motor imagery, as physical practice of the task placed high demands on the body and there was concern of potential injury. Given that pole vaulting involves a complex movement that must be executed with a high degree of precision, Chapter 2 suggests that motor imagery is indeed a valid form of training. The same can be said for several sports or artistic endeavors such as dance. However, a less detailed review of the literature that paid little attention to the experimental tasks used might suggest to a reader that motor imagery is not a viable training method. It is therefore important that motor imagery researchers contextualize their results according to the task used. Importantly, motor imagery is of interest in stroke rehabilitation, and recent Cochrane reviews appear favorable but call for more research [48,49]. It is critical that future research in motor imagery for use in rehabilitation after stroke take seriously what outcome measures they are using. Stroke rehabilitation outcomes are assessed using a wide variety of different measurement tools which may emphasize different aspects of motor behaviour and therefore recovery. For instance, two popular measures of upper extremity movement in stroke recovery research are the Fugl-Meyer Assessment and the Action Research Arm Test. The Fugl-Meyer Assessment is generally considered a measure of impairment (that is, a measure of movement deficits caused by stroke) while the Action Research Arm Test is generally considered a measure of function (that is, the ability of the patient to achieve a movement goal regardless of how the impairment might have affected the movement) [50]. It is possible that motor imagery has differential effects on impairment and function — for example, motor imagery may drive novel motor skill development in a stroke patient to allow them to achieve tasks that are important to them but may have little effect on their impairment. If a clinical trial of motor imagery in stroke measures the Fugl-Meyer Assessment and not the Action Research Arm Test, they may not discover this benefit, resulting in rehabilitation guidelines that do not recommend motor imagery despite its effectiveness — which would be a disservice to the patients recovering from such a devastating event.

5.5. CONCLUSION

Motor imagery has long been a topic of considerable interest in psychology and neuroscience. Its covert nature adds an air of mystique, and the potential applications provide compelling motivation to take the topic seriously. This dissertation focused on investigating whether motor imagery can drive improvements in the execution of movement — as opposed to planning and preparation of movement — as the question has important theoretical and practical implications. The experiments presented here suggest that motor imagery is indeed capable of driving this type of motor skill learning and does so by utilizing existing resources of the motor system but with an emphasis on different computations compared to overt movement. This difference in computational emphasis will give rise to measurable differences in neuroimaging results, behavioural outcomes, and learning. These findings therefore make a valuable contribution to the motor imagery literature as they resolve conflicting interpretations of previous work. As such, these findings also contribute to the broader motor learning literature, particularly with respect to how it may be achieved via motor imagery.

While movement has its effects on the outside, a full appreciation requires that we look inside. Motor imagery research may represent a unique window to understanding the motor system and the brain generally. Carefully designed experiments can leverage the relationship between overt and imagined movements to gain insight on each, particularly how the brain handles covert processes that are challenging to measure. These insights may also inform our understanding of visual imagery, and ultimately, even the nature of thinking. This dissertation limited its scope to understanding whether motor imagery is capable of driving learning of a particular type of movement skill. The findings presented here provided evidence that it is indeed possible, which combined with the existing literature reviewed above demonstrate the breadth of motor imagery's utility. These are questions I've been interested in since I started practicing dance as an undergraduate student majoring in behavioural neuroscience and began a career as a physiotherapist in neurological rehabilitation. I am grateful that this dissertation has allowed me to indulge in this interest for several years. But while I've achieved a greater understanding of this and related topics, I am left with no fewer questions than before. However, I am hopeful that the work presented here will contribute to future research that I will continue to follow, and if granted the opportunity, continue to pursue myself. It is important that this work continues given the potential to inform applications such as rehabilitation, ultimately helping individuals live healthier and happier lives.

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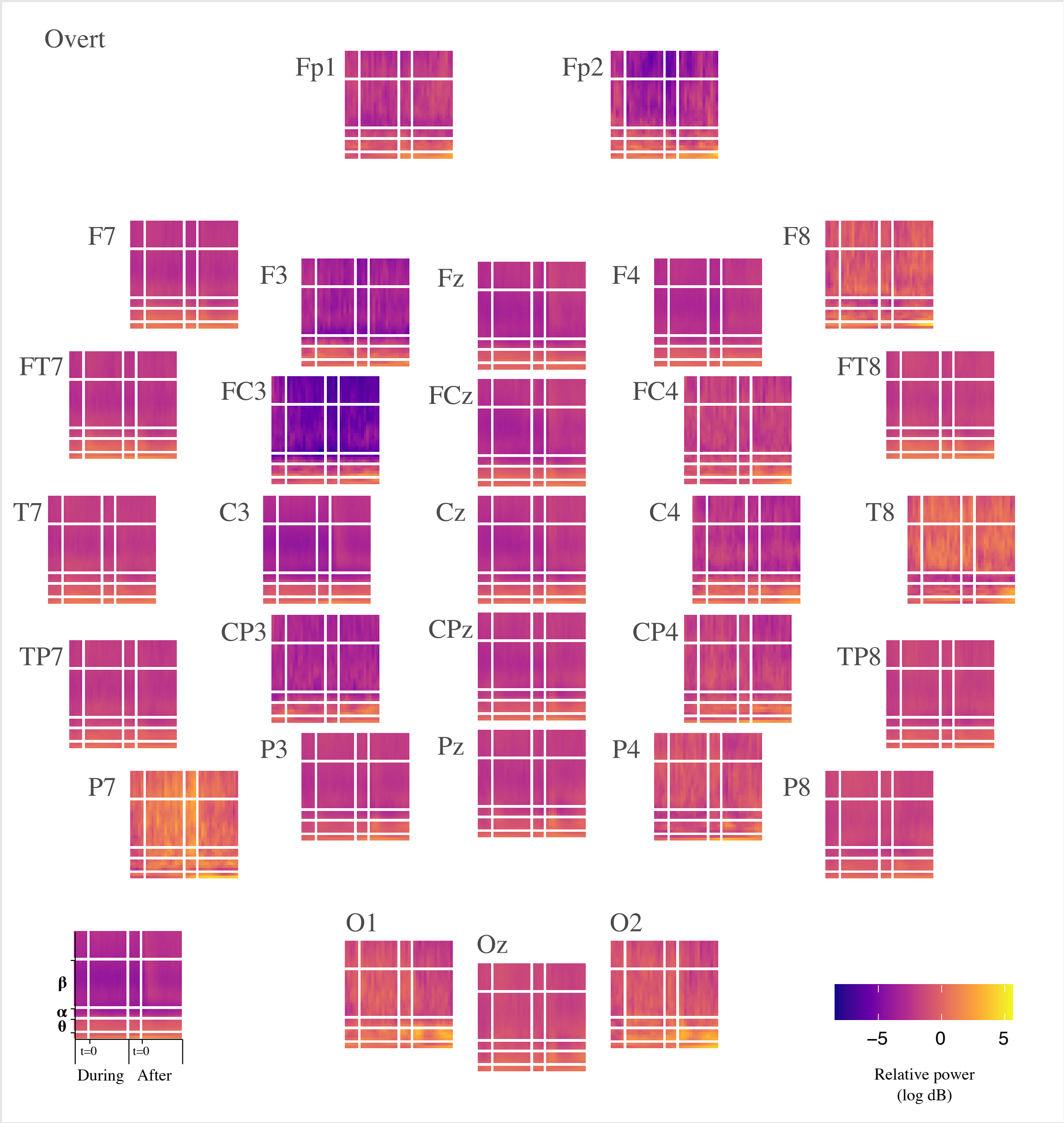
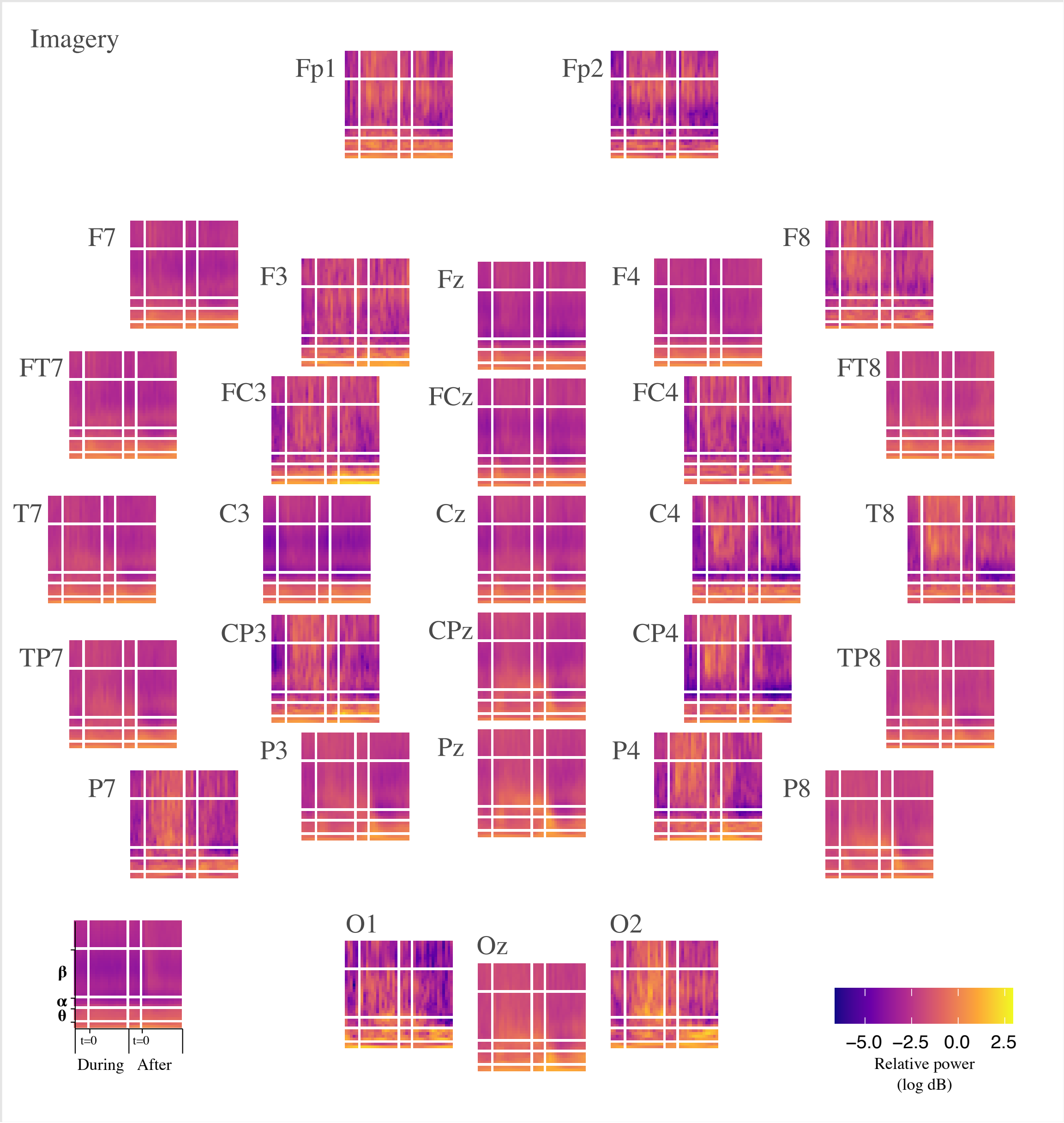
APPENDIX A



Appendix A. Figure 1. Overt group grand average electroencephalography.

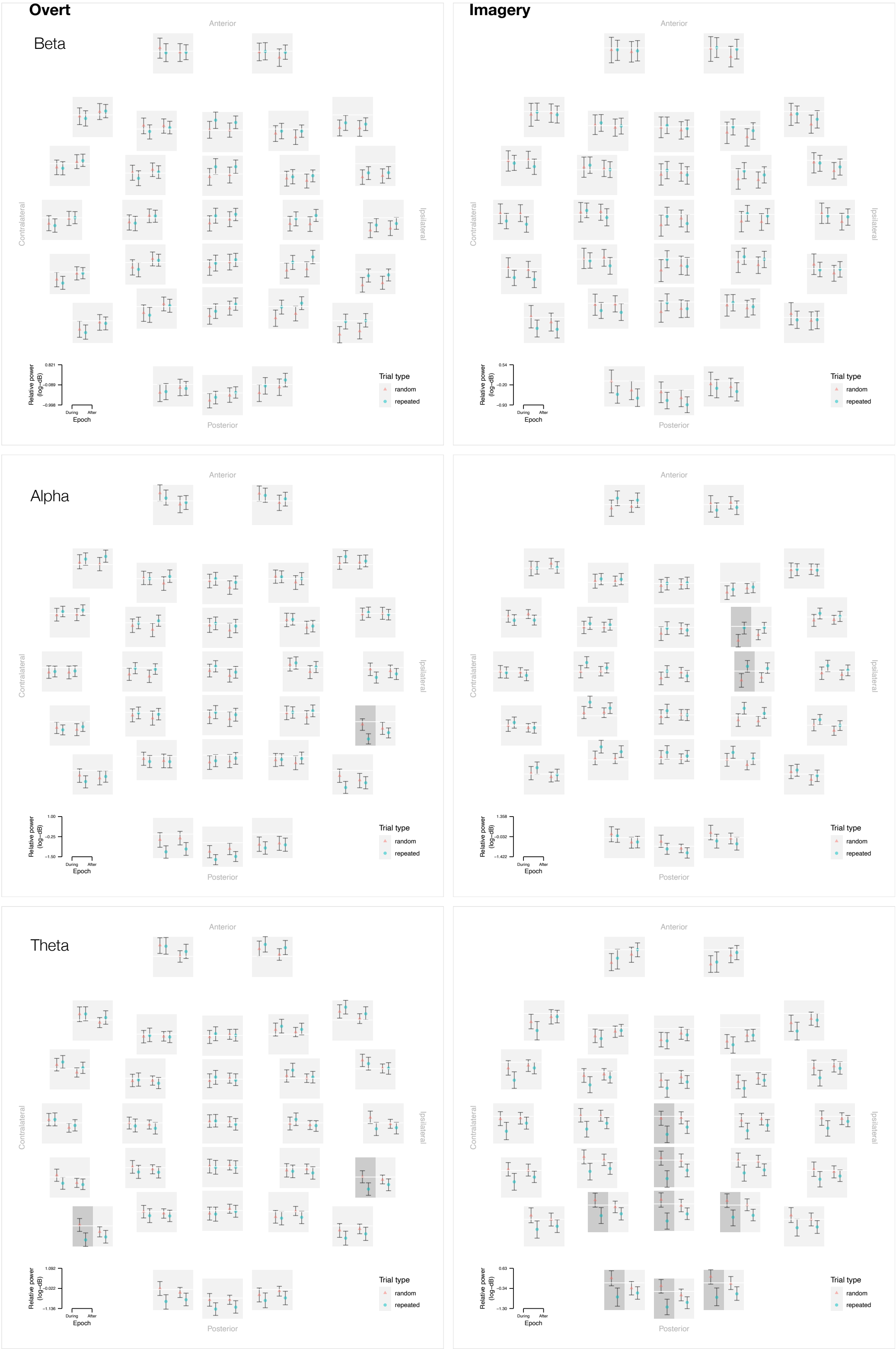


Appendix A. Figure 2. Imagery group grand average electroencephalography.

APPENDIX B

Appendix B. Figure 1. Accuracy related power change by group and frequency band.

Appendix B. Figure 2. Familiarity related power change by group and frequency band.



Appendix B. Figure 3. Low accuracy (bottom 20%) minus high accuracy (top 20%) related power change by group and frequency band.

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