NEURAL MECHANISMS OF MOTOR IMAGERY AND THE NATURE OF IMAGERY-BASED SKILL ACQUISITION

by

Sarah Nicole Kraeutner

Submitted in partial fulfilment of the requirements
for the degree of Doctor of Philosophy

at

Dalhousie University
Halifax, Nova Scotia
August 2019

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS USED

ACF1 – autocorrelation lag-1
ANOVA – analysis of variance
BVE – bivariate variable error
dLPFC – dorsolateral prefrontal cortex
EEG – electroencephalography
EMG – electromyography
ERS/ERD – event-related synchronization/event-related desynchronization
FOV – field of view
fMRI – functional magnetic resonance imaging
IFG – inferior frontal gyrus
IPL – inferior parietal
IPS – inferior parietal sulcus
IUQ – Imagery Use Questionnaire
MEG – magnetoencephalography
MFG – medial frontal gyrus
MI – motor imagery
MIQ-RS – Motor Imagery Questionnaire – Revised Second Version
MRE – mean radial error
PET – positron emission tomography
PP – physical practice
S1 – primary somatosensory cortex
SD – standard deviation
SMA – supplementary motor area
SPL – superior parietal lobe
TE – echo time
TI – inversion time
TR – repetition time
TMS – transcranial magnetic stimulation

ABSTRACT

Motor imagery (MI), the mental rehearsal of movement, is an effective adjunct to physical practice (PP) for driving skill acquisition. While considered analogous to PP, in that a simulation of movement occurs without overt execution, the mechanisms underlying MI are not well understood. This thesis interrogated the mechanisms of MI-based skill acquisition via three research questions: 1) how does expertise modulate MI-related brain activity?; 2) how does the modality of practice (MI vs. PP) modulate performance and MI-based brain activity?; and 3) does MI rely on effector independent encoding to drive skill acquisition? Expertise modulated brain activation during MI similar to PP, in that novice performance during MI was associated with widespread and bilateral activity. Directly comparing MI-related brain activation and performance following MI- or PP-based training showed that refinement of the motor program is less robust in MI owing to a difference in the mechanism underlying learning, suggesting MI is less effective relative to PP for facilitating skill acquisition. By examining resultant patterns of MI-related brain activation and performance of MI-based training applied prior to or following PP-based training, MI was shown to facilitate effector independent encoding, reflected in improvements in the global aspects of movement, central to early stages of skill acquisition. This finding suggests a role for MI as scaffolding for skill acquisition to be facilitated through PP. Evidence generated indicates that, while MI shares neural representations of motor skills, skill acquisition through MI occurs through an alternate mechanism relative to PP, and encoding of information is different between modalities. These findings have implications for how the mechanisms of MI are probed in future work: prior expertise with tasks being performed, and the use of transfer tasks to directly probe effector independent encoding should be considered in lines of questioning related to the mechanisms underlying MI-based skill acquisition. Further, the findings have potential application for how MI is applied in practice: MI is most effective when applied prior to PP, a finding that may explain inconsistencies in its effectiveness in driving skill acquisition noted in the literature.

ACKNOWLEDGMENTS

There are a number of people to whom I would like to express my gratitude to, as contributors to this wild experience. First and foremost, I would like to thank my supervisor, Dr. Shaun Boe, who has not only contributed to my growth as a scientist but also as a human. Shaun, you are the epitome of a mentor. Thank you for your unwavering support, always seeing my potential, and ensuring that I am never standing in the shadows (especially those of tall white men). It has truly been an honour and I look forward to future collaborations, but most importantly, a lifetime of friendship.

I would like to thank my committee members, Drs. Aaron Newman and David Westwood for their guidance throughout my time at Dal. Thank you for all of your scientific input as well as your wit. And to Drs. Gail Eskes and Heather Neyedli, thank you for allowing me to spend time in your labs and learn from you. Your mentorship throughout my time at Dal has been both invaluable and empowering, and I have always looked up to as leaders in your respective fields. I would also like to thank Dr. Tracy Taylor-Helmick for all of the great semesters spent tag-teaming the lecture/lab class. Thank you for taking me under your 'teaching-wing' and I can only hope to one day be half the teacher you are. And to Carl Helmick and Dr. Tim Bardouille, this thesis would not be where it is today without all of your support on the neuroimaging side of things – thank you for downloading slices of your endless systems knowledge to me, and for all of the laughs in all of the (programming) languages.

To my lab mates, past and present – thank you for your friendship and support over the years; the atmosphere fostered within the Boe lab is a rarity, and my official departure will be a bittersweet one. To all the members of the Boe lab who were involved, in any capacity, with the work included in this thesis (as well as the plethora of side projects Shaun and I dreamt up), thank you immensely. These projects would not have been possible without you and all of your hard work.

Thank you to my friends for keeping me sane and giggling throughout this entire ride, whether that's a cheeky ocean dip, a coffee-fueled sunrise, getting "not not lost" on the coast, or sharing a nourishing meal (often with grapes) in this place we are so incredibly lucky to call home.

Last, but most certainly not least, my deepest gratitude to my family. To my sister Katie, thank you for always knowing what and how, and understanding both the grind and the zen. Your outlook on life is my most drawn upon of inspirations. To my parents, Jenny and Paul, I will never be able to say it enough, but thank you, for all of your unconditional love and support. Thank you for instilling in me that I can be whoever and whatever and wherever I want, and that it is okay to take an untraveled path if it means being able to pursue my passions. Because you gave me everything in your power, I know that anything is possible. I am forever grateful to you both.

Chapter 1 : INTRODUCTION

1.0 EXECUTIVE SUMMARY

Skill acquisition is the process of acquiring or strengthening a motor skill via changes in the brain (termed “plasticity”) that result from repetitive practice and the provision of feedback (Fitts and Posner, 1967; Newell; Dayan and Cohen 2011). At the outset of skill acquisition, environmental and sensory stimuli is integrated with an understanding of task goals, generating an abstract representation of the skill (termed “effector independent encoding”; Gallivan et al., 2011; Hikosaka et al., 2012; Verwey et al., 2014). Through repeated practice and thus activation of the neural substrates that underlie task performance, this representation is mapped to a specific effector (i.e., the effector used in the task; Grafton et al., 1998; Bapi et al., 2000; Gallivan et al., 2011). Further, through practice the motor program undergoes alterations via an error detection and correction mechanism that relies on a comparison of the intended consequences of the movement with actual movement outcomes derived from sensory feedback (Wolpert et al., 1998; Bastian, 2006). Ultimately, as skill acquisition is achieved (i.e., performance becomes more consistent, efficient, quick, and accurate), shifts in brain activation occur that reflect a decreased reliance on neural substrates that underlie error detection and correction, and an increase in activation of substrates that relay the motor command to the muscles.

While physical practice (PP) is recognized as the primary approach to skill acquisition, motor imagery (MI), the mental rehearsal of a motor task (Jeannerod, 1995), is an effective adjunct to driving skill acquisition in numerous disciplines (e.gs., sports, music, and rehabilitation; Wulf et al., 2010; Schuster et al., 2011; Moran et al., 2012; Brown and Palmer, 2013). Motor imagery has long been considered analogous to PP, in that MI shares mechanisms (i.e., processes that allow the motor program to be generated and/or updated) and neural representations with PP to facilitate a simulation of the movement without execution (Jeannerod, 1994; 2001). However, despite a wealth of evidence supporting the effectiveness of MI as a secondary modality of skill acquisition, its neural mechanisms remain largely unexplored. Further, owing to the lack of overt execution in motor imagery and thus the absence of feedback about task performance, we lack critical knowledge related to the nature of MI-based skill acquisition.

Motivated by the lack of evidence related to the neural mechanisms underlying MI coupled with our incomplete understanding of the nature of MI-based skill acquisition, this thesis addressed the following research questions via three experiments: 1) how does expertise modulate MI-related brain activity?, 2) how does the of practice (MI vs. PP) modulate performance and MI-based brain activity?, and 3) does MI rely on effector independent encoding to drive skill acquisition?

The first experiment utilized a mixed within- and between-group design in which 1) brain activity of experts (i.e., varsity athletes) performing MI of a sport-specific task vs. a novel task was compared, and 2) brain activity of experts and recreational controls during MI of a task that all groups had a similar degree of expertise of was compared. Results demonstrated that novice performance is associated with widespread activity encompassing bilateral frontal and parietal regions that resembles a typical pattern of brain activity during novice physical performance. Importantly, the level of (physical) expertise should be considered in neuroimaging investigations of MI, as resulting patterns of brain activation observed may reflect a novice level of MI performance vs. task-specific patterns.

The second experiment utilized a longitudinal between-group design, in which brain activation and performance outcomes were compared before and after five days of training of a complex motor skill via PP or MI. Results showed that greater activation in regions critical to refining the motor program were observed in the PP vs. MI group post-training, and MI led to smaller improvements in performance relative to PP. Thus, relative to PP, MI-based training did not drive robust changes in brain activation and was inferior for realizing improvements in performance. Critically, findings from this experiment advance our understanding of the mechanisms of MI in two ways: 1) that refinement of the motor program is less robust in MI owing to a difference in the mechanism underlying learning; and 2) different information is encoded in MI relative to PP.

The final experiment utilized a longitudinal crossover design, in which improvements in performance and changes in brain activation were compared when an equivalent bout of MI was applied either prior to, or after PP-based training. Results showed that MI drives changes in global aspects of a movement, reflecting encoding critical to forming the abstract representation of the movement, central to early stages of skill acquisition. Further, that these improvements were only observed when MI was applied prior to PP and following training (i.e., after all ten sessions) indicates that the encoding driven via MI acts as scaffolding for which mapping of this representation to a specific effector can be readily facilitated. This experiment provides critical insight as to how a simulation of movement is able to drive skill acquisition in the absence of feedback: MI relies on an alternate error detection and correction mechanism relative to PP that relies on a comparison of intended movement outcomes with simulated feedback representations.

Overall, the present dissertation provides unique knowledge pertaining to the neural underpinnings of MI and the nature of MI-based skill acquisition. Driving our understanding of MI as a modality of practice forward, findings of the present dissertation have important implications for both the way the mechanisms of MI are probed in future investigations and the application of MI for skill acquisition in health and disease. Specifically, prior expertise with tasks being performed, and the use of transfer tasks to directly probe effector independent encoding should be considered in lines of questioning related to the mechanisms underlying MI-based skill acquisition. Further, the findings have potential application for how MI is applied in practice: MI is most effective when applied prior to PP, a finding that may explain inconsistencies in its effectiveness in driving skill acquisition noted in the literature.

1.1 GENERAL INTRODUCTION

1.1.1 Motor skill acquisition

Motor skill acquisition is the fundamental process of acquiring or strengthening a motor skill, in which executed movements become more efficient, quick, and accurate. With repeated practice, novices move along the expertise continuum, realizing improvements in performance. Motor skills vary in their complexity and in the time required to gain expertise – for instance, learning a key-press sequence quickly and accurately to sinking basketball free throw or executing a dart throw with precision have differing levels of complexity and timescale for achieving proficiency in performance. Motor skill acquisition requires the integration of a number of different processes, including cognitive, perceptual, and motor processes, depending on the nature of the task to be learned (Newell, 1991; Wulf et al., 2010; Taylor and Ivry, 2012) . In the classic framework of motor skill acquisition, Fitts and Posner (1967) theorized that motor skill acquisition occurs as a result of repetitive practice over three stages: 1) the cognitive stage, 2) the associative stage, and 3) the autonomous stage. In the cognitive stage of skill acquisition, it is thought that an individual consolidates their understanding of ‘what to do’ in terms of task goals and movement elements. In this stage, cognitive and perceptual processes are heavily relied on as environmental stimuli and features of the movement are processed to create a perceptual representation of the movement, typically characterised by inefficient and inaccurate performance of the motor skill. Notably, this form of encoding is not specific to an effector, but rather can transfer between effectors, and thus is termed 'effector independent' encoding. In the associative stage, the actual motor program (i.e., the ability to perform consistent, accurate movements) is formed. In this stage, stimulus-response associations are strengthened as the perceptual representation is integrated with a motor representation (i.e., movement goal) to create the motor program. Once the motor program is generated, this information becomes mapped to the specific effector (i.e., effector dependent encoding) and refined with repeated practice and feedback. Finally, in the autonomous stage, the skill is carried out with little conscious effort (Fitts and Posner, 1967). Specifically, as the individual approaches the 'end' of the expertise continuum and robust improvements in performance are realized, little cognitive effort is required to perform the motor skill, and external factors such as the environment have minimal influence on performance (Fitts and Posner, 1967; Taylor and Ivry, 2012).

1.1.2 Neural networks underlying expertise

It is well established that brain regions including the primary motor cortices, fronto-parietal regions, supplementary motor area (SMA), and cerebellum, are associated with motor planning, preparation, and execution, establishing the neural network that underlies successful motor task performance (Newell, 1991; Hikosaka et al., 2002; Dayan and Cohen, 2011; Hardwick et al., 2013). Repetitive practice drives synaptic plasticity in these regions, facilitating changes within the network as the skill becomes consolidated (Fig. 1.1; Ungerleider et al., 2002; Doyon and Benali, 2005; Dayan and Cohen, 2011). In general, as improvements in performance are realized, moving along the expertise continuum is associated with a shift in brain activity – in that activity overall becomes more lateralized (to a contralateral pattern of activity in a unimanual task), and focal. A general decrease in reliance on cerebellar and striatal circuits are observed, and increased recruitment of primary motor and somatosensory cortices is associated with skill expertise as the autonomous stage is achieved (Fig. 1.2; Poldrack et al., 2005; Yarrow et al., 2009; Nakata et al., 2010; Dayan and Cohen, 2011). Taken together, expertise is characterised by a generally contralateral and focal pattern of cortical brain activity, regardless of the skill.

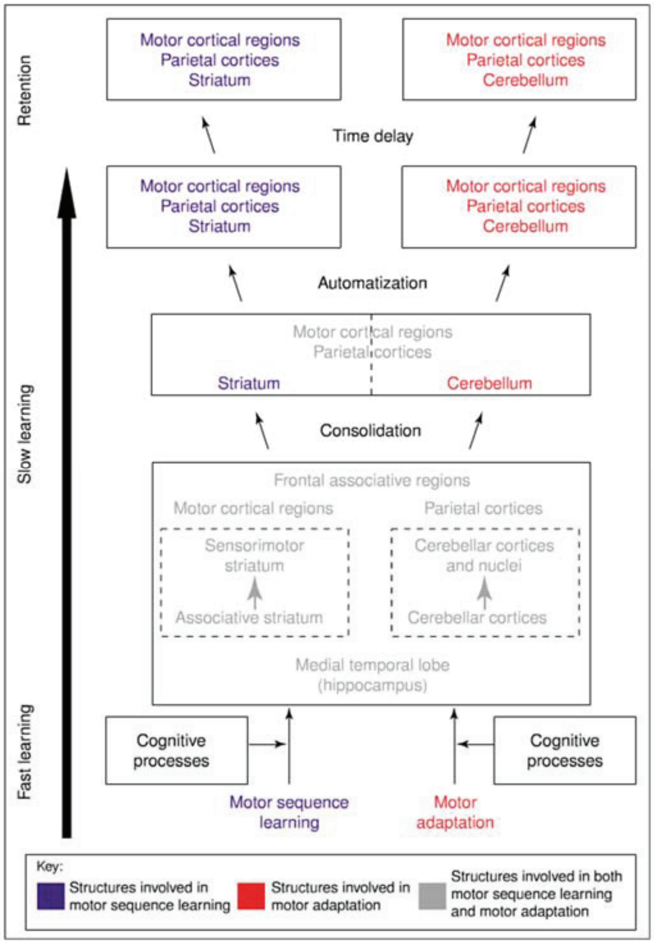


Figure 1.1 Neural circuitry underlying motor learning. As skill expertise is gained, there is a general shift from frontal regions and reliance on cerebellar and striatal circuits to increased recruitment of primary motor and somatosensory regions. Taken from Doyon and Benali (2005).

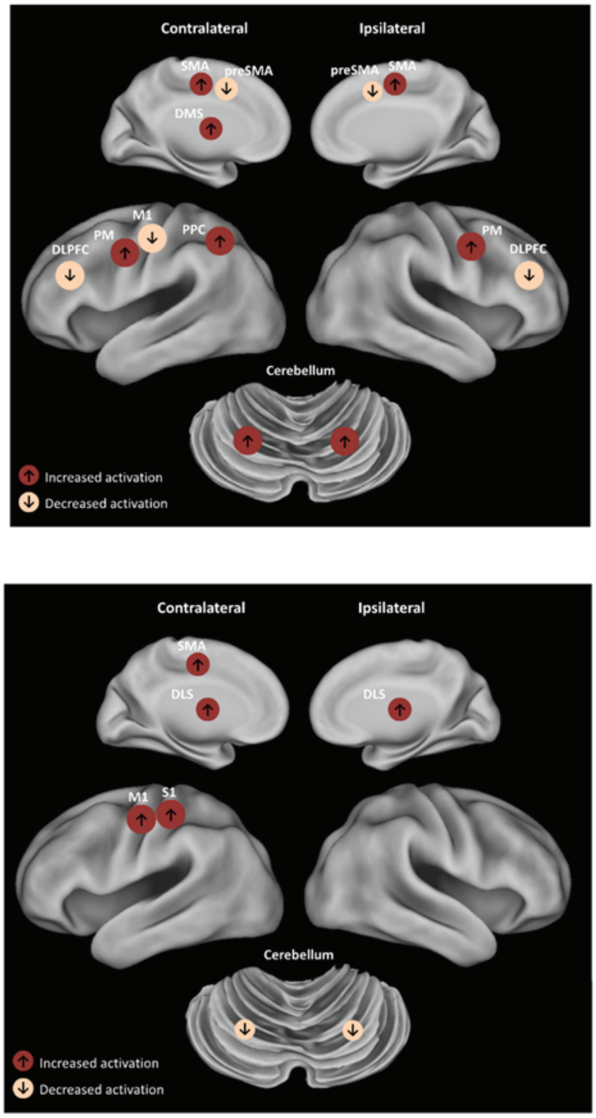


Figure 1.2 General shifts in patterns of brain activation observed during fast (top) and slow (bottom) skill acquisition, driven through physical practice. During fast skill acquisition, greater reliance on the cerebellum and supplementary motor area is observed. During slow skill acquisition, cerebellar activity decreases as increased recruitment of primary motor and somatosensory regions is observed. Adapted from Dayan and Cohen (2011).

1.1.3 Effector dependent encoding and the primary motor cortex

Consistent activation of the primary motor cortex is observed in neuroimaging studies of motor tasks (see Hardwick et al., 2013 for a meta-analysis), and task expertise is reflected in responses of primary motor cortex neurons (typically, contralateral to the effector in a unimanual task; (Pascual-Leone et al., 1994, 1995; Matsuzaka et al., 2007; Dayan and Cohen, 2011) Repetitive practice drives changes in the topography of the primary motor cortex, in both primates and humans. Nudo et al. (1996) demonstrated that representations within primate primary motor cortex adapted to represent specific aspects of the skill being trained. In particular, after assessing cortical reorganization of primary motor cortices following multiple days of training on an object retrieval task requiring two different sets of forelimb movements, it was shown that training a task involving skilled digit use led to the expansion of the representation for the digits. In contrast, training on a task requiring forelimb movements (but not skilled use of the digits) led to an expansion of the forearm representation (Nudo et al., 1996). In alignment with this work, Pascual-Leone et al. (1995) assessed cortical reorganization in human primary motor cortex following five days of practice of a sequence-learning task (Fig. 1.3). It was shown that employing sequence-learning tasks results in changes in the motor output map (i.e., associated region of the primary motor cortex) associated with the digits and hand involved in the task. Thus, it follows that neuroimaging work (largely employing positron emission tomography (PET) and functional magnetic resonance imaging (fMRI)) has shown that activation of primary motor cortex increases as later stages of learning are achieved (Dayan and Cohen, 2011).

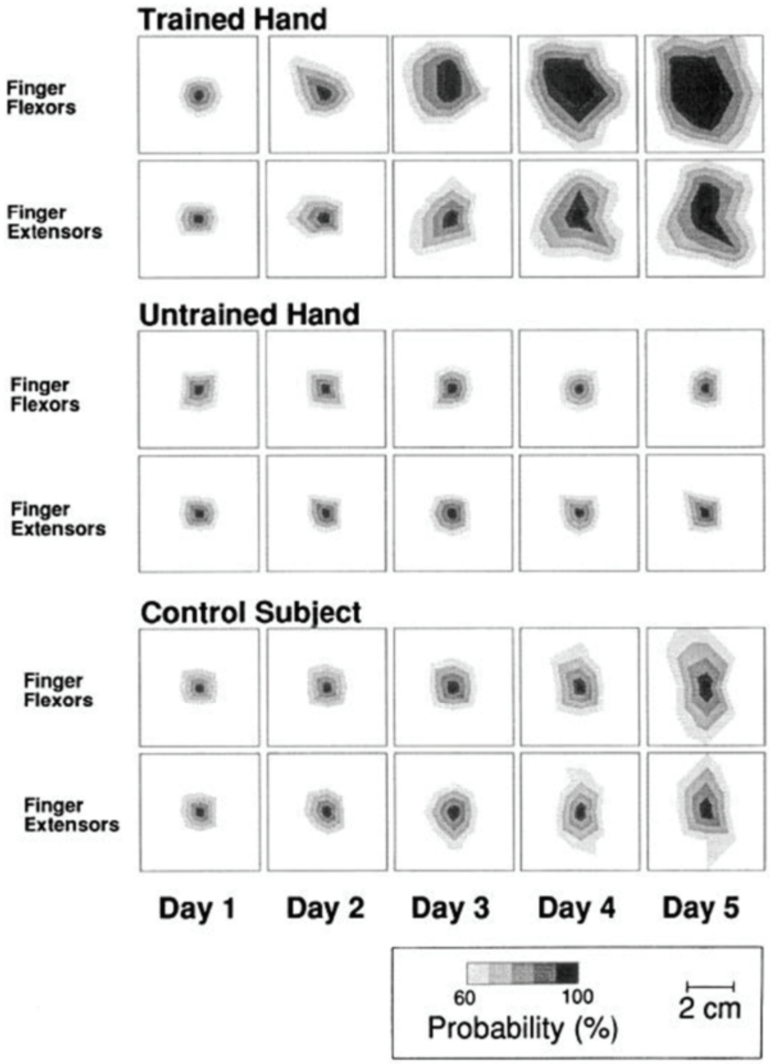


Figure 1.3 Motor output maps (i.e., associated region of the primary motor cortex) for the trained vs. untrained hand over five days of a sequence (piano-based) task. Taken from Pascual-Leone et al. (1995).

With subsets of neurons that send output to different effector groups, the primary motor cortex is critical for effector dependent encoding (Grafton et al., 1998; Bapi et al., 2000; Ungerleider et al., 2002; Gallivan et al., 2011). Neurons localized to this region are tuned to the kinematics of a movement (Georgopoulos et al., 1986; Georgopoulos, 1990; Ashe and Georgopoulos, 1994), and this region encodes specific aspects of the movement such as force and timing parameters (Hikosaka et al., 2002; Apolinário-Souza et al., 2016). Specifically, through examination of discharge rates of neurons in monkey motor cortices during a task in which the animals moved a handle in different directions in response to visual cues, it was shown that the direction of the arm movements could be inferred from the neuronal activity (Georgopoulos et al., 1986; Ashe and Georgopoulos, 1994). These results have been replicated in humans by assessing the reduction of brain activation obtained via fMRI in a specific region during a task (termed "BOLD adaptation"), which reflects the extent to which the same population of neurons is engaged and thus adapt over time (Cowper-Smith et al., 2010). Greater BOLD adaptation was observed when consecutive movements were made in the same direction relative to consecutive movements made in different directions, indicating that human primary motor cortex encodes the direction of movement similar to non-human primates (Cowper-Smith et al., 2010).

During a single session of sequence training, increases in primary motor cortex activity have been linked to the effector employed in training (Seitz et al., 1990; Grafton et al., 1992; Jenkins et al., 1994; Karni et al., 1998; Lehéricy et al., 2005). Further, sequence-specific activation shifted following transfer to a different effector (i.e., shifted from executing distal finger movements to proximal arm movements; Grafton et al., 1998). Thus, the authors concluded that the primary motor cortex was not encoding information pertaining to the structure of the sequence itself (i.e., the abstract representation), and instead was receiving this information from upstream areas (e.gs., SMA or posterior parietal regions) and mapping it to the specific effector. This conclusion is supported through work by Bapi et al. (2006), who assessed sequence-specific brain activation using fMRI, whereby participants trained on the task by pressing corresponding buttons on a keypad that matched cues appearing on a matching keypad displayed a screen. Participants then engaged in a test phase where they were tested under three conditions: a control condition that matched training, a motor condition where the keypad was rotated such that participants performed the same finger movements as the training condition yet the spatial organization of the targets differed, and a visuospatial condition where the keypad was rotated such that the spatial organization of the targets matched the training condition but the finger movements differed (Bapi et al., 2000, 2006). Relative to the control condition, activation localized to the primary motor cortex was only observed in the motor condition, whereas the visuospatial condition engaged predominantly frontal and parietal regions. Collectively, task-dependent changes are reflected in the organization and response of neurons localized to the primary motor cortex (Georgopoulos et al., 1986; Ashe and Georgopoulos, 1994; Pascual-Leone et al., 1994, 1995; Bapi et al., 2006; Matsuzaka et al., 2007; Apolinário-Souza et al., 2016).

1.1.4 Effector independent encoding and the dorsal stream pathway

It is well-established that activation in frontal and parietal areas are critical to integrating stimuli and features of the movement into the motor representation. In particular, there is a large body of evidence related to a pathway of information transfer from posterior visual to parietal areas with output to premotor areas, termed the dorsal stream of action processing (Fig. 1.4; Goodale and Milner, 1992; Rizzolatti and Matelli, 2003; Binkofski and Buxbaum, 2013). This pathway facilitates visuospatial processes and visuomotor transformations necessary for goal-directed and visually-guided actions to be executed (Goodale and Milner, 1992; Goodale and Westwood, 2004; Buxbaum et al., 2006, 2007; Binkofski and Buxbaum, 2013). Evidence from lesion studies and studies employing transcranial magnetic stimulation (TMS; a non-invasive form of brain stimulation that can be used to temporarily inhibit focal brain activity prior to a task, or that can be used to disrupt online processing within a brain region during a task), supports the critical role of this pathway in visually guided actions, whereby damage to posterior parietal regions results in deficits in motor control for reaching tasks (i.e., impaired accuracy of the reach), tool-use, and inferring the functional use of objects and/or tools from its structure (Rushworth et al., 1997, 2001; Weiss et al., 2001; Buxbaum et al., 2005, 2006, 2007; Binkofski and Buxbaum, 2013).

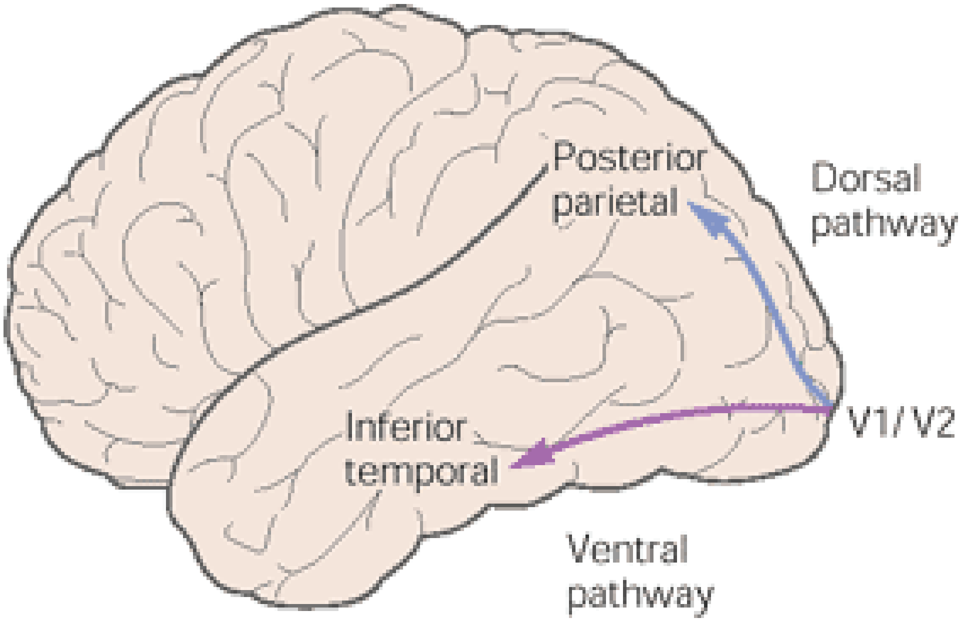


Figure 1.4 Depiction of the dorsal visual pathway, indicated in blue. Posterior parietal regions, including the inferior and superior parietal lobule, are implicated in visuospatial processes and visuomotor integration during visually guided actions. Taken from Kandel et al. (2000).

The contribution of these areas to visuospatial processes and processing perceptual aspects of the movement suggests that these regions are critical to effector independent encoding during motor skill acquisition (i.e., as the perceptual and spatial information is integrated with the movement goal; Hikosaka et al., 2002; Gallivan et al., 2011). Specifically, a cortical loop comprised of posterior parietal (encompassing the inferior and superior parietal lobes; IPL/SPL) and prefrontal regions is proposed to underlie the encoding of global aspects or spatial parameters of the movement, and perceptual cues are mapped to movement goals such that learning can transfer to skills that have the same global structure but not specific elements (Fig. 1.5; Hikosaka et al., 2002). Indeed, in the above noted sequence studies (Grafton et al. 1998; Bapi et al., 2006), it was shown that visuospatial sequence representations engaged predominantly prefrontal and parietal cortices (Bapi et al., 2006), and that sequence-specific activation was linked to posterior parietal regions (Grafton et al., 1998). In these studies (Grafton et al. 1998; Bapi et al., 2006), it was concluded that these regions were responsible for creating the abstract representation of the sequence.

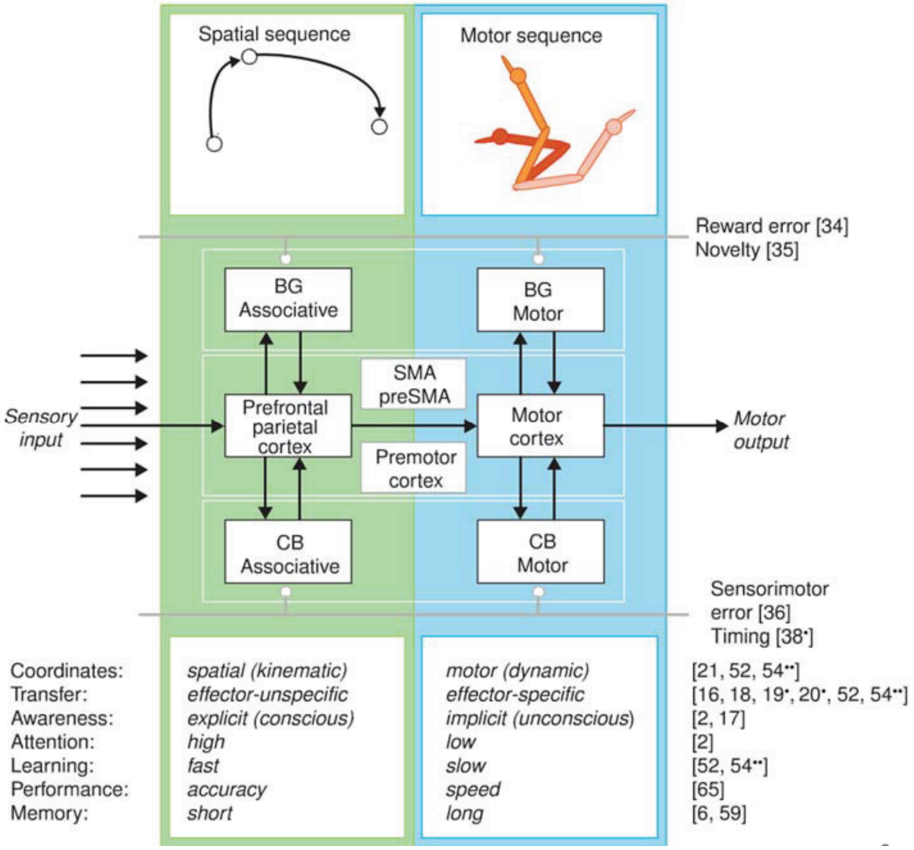


Figure 1.5 Neural circuitry underlying effector independent (or ‘effector-unspecific’) and effector dependent (or ‘effector-specific’) encoding during sequence learning. A circuit comprised primarily of prefrontal and parietal areas is thought to underlie effector independent encoding (as assessed through the acquisition of spatial sequences, in which the encoding is not specific to an effector), while a circuit that relies predominantly on the primary motor cortices is thought to facilitate

effector dependent encoding (as assessed through the acquisition of motor sequences, in which the encoding is specific to the effector used in the task). Taken from Hikosaka et al. (2002).

Further, a study conducted by Gallivan and colleagues (2011) employed fMRI during a task where participants were asked to perform a reach or saccade to one of two different spatially located targets. Brain activation was assessed at three different phases of the movement: preview, whereby the targets appeared; plan, whereby the participants received an instruction regarding the movement they were to perform; and execute, whereby the participants performed the movement to the appropriate target (Gallivan et al., 2011). It was shown that activity during the planning phase localized to the right mid and left posterior inferior parietal sulcus (i.e., near the postcentral gyrus or the trans occipital sulcus, respectively; IPS) predicted both effector-specific and spatial-specific response information, in that the target that would be acted upon in the execute phase was predicted, as well as the effector to be used. Further, only the spatial location of the target to be acted upon in the execute phase was encoded by the left mid IPS, highlighting the critical role of this region in effector independent encoding. Importantly, activity in these regions was contrasted with activity in dorsolateral prefrontal cortex (dLPFC) and primary motor cortices, in which activity only predicted the effector to be used in the task but not the spatial location of the target to be acted upon; thus highlighting the effector dependent nature of activity in these regions (Gallivan et al., 2011).

In light of the notion that this pathway is critical to the formation of perceptual and motor representations required to execute the skill, it follow that increases in activation within these areas are observed in the early stages of motor skill acquisition, as the individual consolidates their understanding of ‘what to do’ in terms of task goals and movement elements, and the motor program is generated. Indeed, a single-session of sequence training led to increased activation within frontal and parietal areas (Grafton et al., 1998, 2002; Floyer-Lea and Matthews, 2005). In contrast, no differences in activation within these areas were observed pre/post three weeks of training, indicating that once the understanding of the movement elements and motor representation has been established and refined, the need for resources related to spatial processing are reduced.

1.1.5 Cerebellum in skill acquisition

Throughout motor skill acquisition, output of cerebellar neurons is associated with error detection/correction whereby the predicted consequences of the movement (efference copy) are compared to actual movement outcomes (reafference) in a forward model to update the motor program (Fig. 1.6; Miall and Wolpert, 1996; Wolpert et al., 1998; Bastian, 2006; Popa et al., 2012). Specifically, refinement of the motor program is thought to occur via internal comparisons whereby the predicted consequences of the movement (efference copy) are compared to actual movement outcomes (reafference) in a forward model (Miall and Wolpert, 1996; Bastian, 2006; Shadmehr et al., 2010). Ultimately, this comparison allows us to detect and correct errors, resulting in refinement of the motor program with repeated execution of the movement (Fig. 1.6; Miall and Wolpert, 1996; Bastian, 2006; Shadmehr et al., 2010).

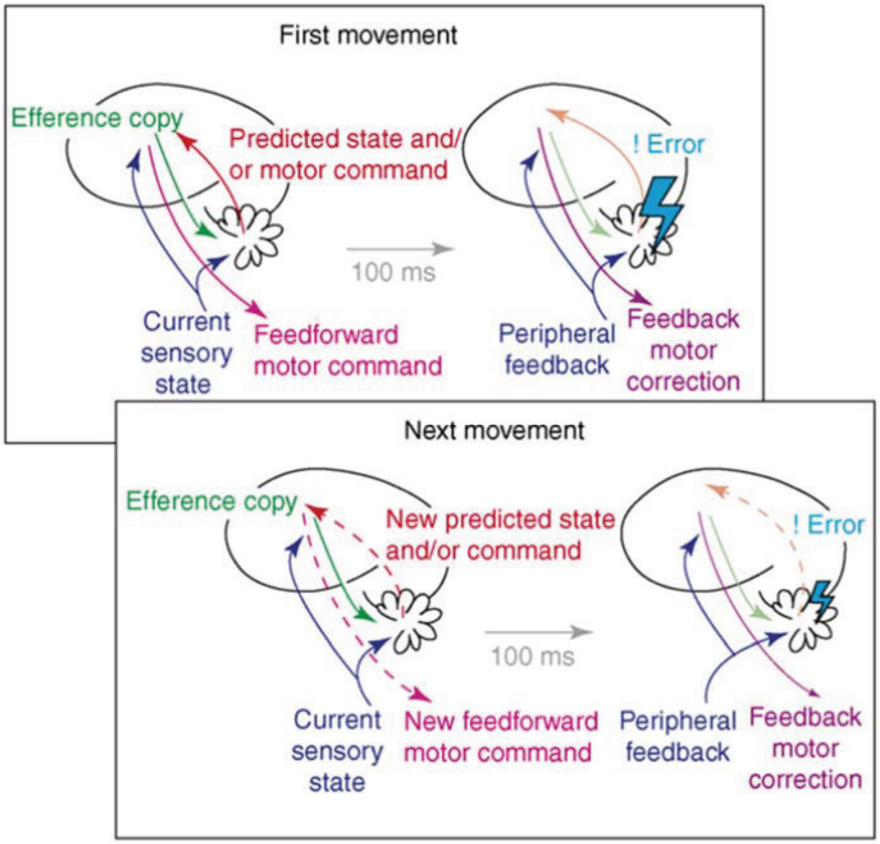


Figure 1.6 Illustration of forward models in the cerebellum that underlie error detection/correction mechanisms during motor skill acquisition. Detection of errors during the current movement occurs via a comparison between the predicted (efference copy) and actual sensory (reafference) consequences of the movement. Errors in the feedforward command during subsequence movements are then reduced, and the motor program is updated as skill acquisition occurs. Adapted from Bastian et al. (2006).

In studies conducted where cerebellar neurons were recorded in primates during reach and grasp tasks (Espinoza and Smith, 1990; Smith et al., 1993), tracking tasks (Popa et al., 2012, 2013; Popa and Ebner, 2018), and during passive vs. self-generated movements (Brooks and Cullen, 2013), neuronal activation was observed immediately prior to and after movement onset, suggesting a key role in predicting and realizing kinematic consequences of the movement (Blakemore and Sirigu, 2003). For instance, Popa et al. (2012), monitored activity of Purkinje neurons (i.e., the primary output pathway of the cerebellum to other regions including the primary motor cortex) in a tracking task where the animals were trained to track a moving target on a screen by moving a cursor. In demonstrating neuronal output in response to errors that followed the movement, as well as neuronal output immediately prior to the movement, it was concluded that the cerebellum is critical in integrating predictive and feedback representations (Popa et al., 2012). Further, Brooks and Cullen (2013) examined activity of cerebellar neurons between expected and unexpected sensory inputs, by inducing passive movements of the head and body of monkeys while the animals made voluntary movements. Specifically, by inducing unexpected sensory inputs during the movements, the predictions made by the forward model are poorly matched with the resulting feedback. In contrast, when the animal executes a movement voluntarily with similar sensory stimulation, the predictions made by the forward model were well-matched with the resulting feedback. Interestingly, neuronal output was modulated by the match between the predicted consequences and feedback in that the cells were highly responsive to the unexpected sensory input yet did not respond to voluntary movement. Taken together, this body of work supports the role of the cerebellum in both generating the movement prediction and providing the motor command that will cause a desired change in the forward model to update the motor program (Wolpert et al., 1998; Blakemore and Sirigu, 2003; Shadmehr et al., 2010; Shadmehr, 2018).

Findings from the above-noted primate studies are supported by work in humans – neuroimaging studies examining cerebellar activation during movement highlight the involvement of this region in forward models, both for predicting movement consequences and processing reafferent information (Gao et al., 1996; Jueptner et al., 1997; Blakemore et al., 1998). For instance, greater cerebellar activation was observed when comparing brain activation during a movement that had a tactile consequence vs. an identical movement that did not have a tactile consequence. Thus, the authors concluded that cerebellar activity depends on specific consequences of the movement (Blakemore et al., 1998). Further, cerebellar lesions are known to result in dyscoordination of movements and the inability to adapt reach movements to motor perturbations (for reviews see Wolpert et al., 1998; Blakemore and Sirigu, 2003). For instance, Müller and Dichgans (1994) employed a pinch-grip task whereby participants were asked to lift objects of varying loads (and thus had to adapt to the load of the object), requiring accurate timing of a pinch-grip and lift movements. Participants with cerebellar lesions (ipsilateral to the effector used in the task) exhibited a lack of coordination in the movements in that an increase in the onset latency of lift force was observed after the pinch movement was made. Thus, participants were incorrectly predicting the sensory consequences of the movement and thus had to adjust online in order to perform the lift (Müller and Dichgans, 1994).

With respect to motor skill acquisition, it follows that increases in cerebellar activation are observed in the early (i.e., 'fast') stages, as changes to the motor program are required on a trial-by-trial basis as performance has yet to plateau and large changes to the motor program are desired (Seitz et al., 1994; Ungerleider et al., 2002; Lacourse et al., 2004; Doyon and Benali, 2005; Shadmehr et al., 2010; Dayan and Cohen, 2011; Shmuelof et al., 2014). However, as expertise is achieved and the motor program requires less refinement, it follows that a decrease in cerebellar activation is observed (Dayan and Cohen, 2011; Boe et al., 2012). Interestingly, Boe et al. (2012) demonstrated a decrease in cerebellar activity over a single-session of training on a bilateral visuomotor task where participants moved a cursor towards a target by gripping bulbs with varying forces. In this task, it is likely that both a refined motor program and accurate forward model were achieved within the single-session of training. Similarly, a decrease in cerebellar activation was observed pre/post 30 min of training on a sequence task, whereby the limited complexity of the task likely allowed participants to gain expertise with minimal training (Doyon et al., 2002). These findings are in line with evidence showing decreases in cerebellar activity over multiple training sessions of complex tasks (i.e., whereby the motor program is still being refined after a single session or it takes a number of weeks for expertise to be achieved; Dayan and Cohen, 2011), and the authors suggested that the decrease observed reflected a diminished need to modify the motor program or forward model as desired changes are no longer necessary as performance improves (Doyon et al., 2002; Boe et al., 2012). Thus, cerebellar activity is directly linked to expertise, in that the extent to which modifications to the motor program/forward model are required modulates cerebellar activation.

1.1.6 Supplementary motor area in skill acquisition

The SMA is a key structure implicated in motor planning and execution (Tanji and Shima, 1996; Nachev et al., 2008; Dayan and Cohen, 2011; Flash and Bizzi, 2016), ultimately relaying the motor command to the primary motor cortex for output to the effector (Roland et al., 1980; Tanji and Kurata, 1982; Tanji and Shima, 1994; Cunnington et al., 2003). Recording in primates demonstrate that SMA activity occurs immediately prior to movement onset, generating a preparatory state for the impending (and forthcoming) movements (Roland et al., 1980; Tanji and Kurata, 1982; Tanji and Shima, 1994; Cunnington et al., 2005). For instance, through recordings of neurons in primates during a task that involved forelimb and hindlimb movements, the extent to which neurons localized to SMA vs. neurons localized to primary motor cortex was coupled with movement onset was examined (Tanji and Kurata, 1982). While neuronal output in both regions increased prior to movement onset, a weaker correlation between SMA output and reaction time of the animal resulted relative to the primary motor cortex. In other words, SMA activity preceded both movement onset and primary motor cortex activity. Further, SMA neurons showed greater coupling with sensory stimuli that cued a motor response (i.e., lights that turned on to signal the animal that a successful movement had been made or to cue the animal to make the next movement) than neurons in the motor cortex.

Prior work has also demonstrated that this region is implicated in transforming desired kinematics to be used in the task to the set of forces exerted by the effectors (termed the 'kinematics-to-dynamics transformation'; Li et al., 2001; Padoa-Schioppa et al., 2002, 2004). Specifically, through SMA recordings in primates during a visually-guided reaching task where the animals were required to manipulate a robotic arm either with or without the application of an external force field (i.e., external perturbations; Padoa-Schioppa et al., 2004). When required to adapt to the external perturbation, activity in the SMA changed in that a greater number of SMA neurons responded to the stimuli (i.e., were directionally tuned to the stimuli). The authors concluded that as adapting to the perturbation requires a change in motor planning and/or the preparatory state for the movement, activity of SMA neurons thus reflect the dynamics of the upcoming movement. Importantly, similar findings have been demonstrated in humans (Cunnington et al., 2003; Nachev et al., 2008) – scalp recordings have revealed that an event-related potential, termed the Bereitschaftspotential, that peaks immediately prior to movement onset and is thought to represent cortical activity related to motor preparation, is localized over SMA (Deecke and Kornhuber, 1978; Cunnington et al., 2005; Nachev et al., 2008), and SMA activity is shown to precede that of the primary motor cortex during motor execution as evidenced through fMRI studies employing sequence tasks (Fig. 1.7; Weilke et al., 2001; Cunnington et al., 2003).

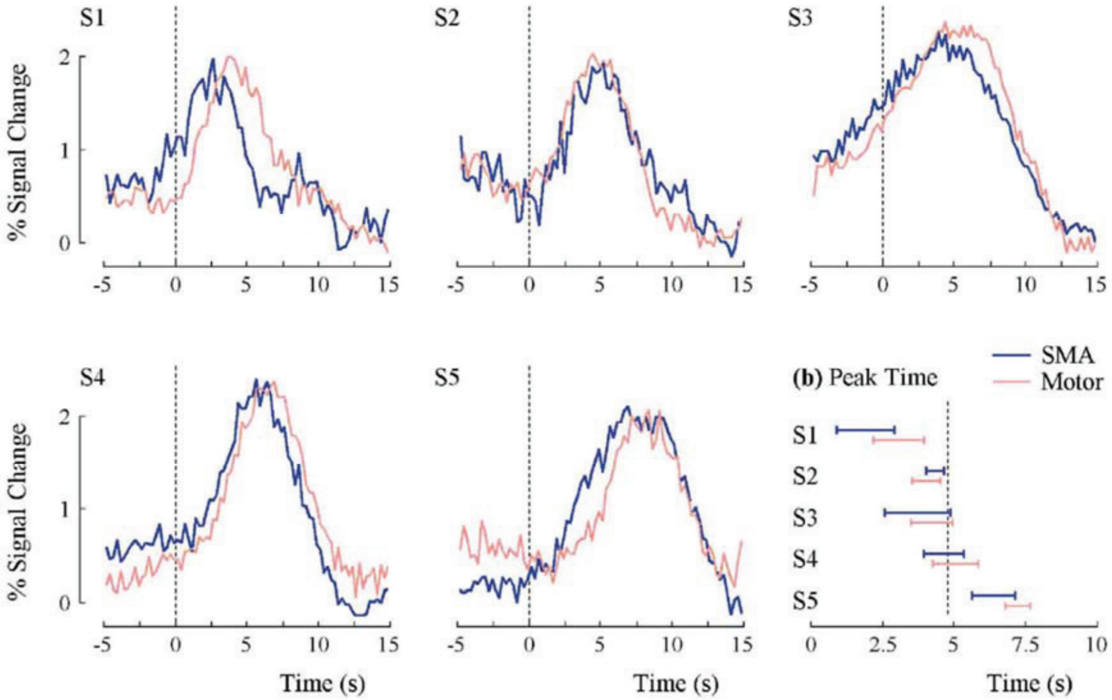


Figure 1.7 Single subject analysis of a) the mean time course of activated voxels within supplementary motor area (blue) and primary motor cortex (pink), where movement onset is represented by the dotted line (Time = 0), and b) the mean and standard deviation of voxel peak times, where the dotted line represented the peak of the reference hemodynamic response functions. While a large degree of variability in peak response times was observed across subjects, and time courses between supplementary motor area and primary motor cortices overlapped, supplementary motor area activity is shown to precede primary motor cortex activity. Adapted from Cunnington et al. (2005).

Increased SMA activity typically observed during both the early (i.e., 'fast') and later (i.e., 'slow') stages of motor skill acquisition (Ungerleider et al., 2002; Dayan and Cohen 2011) is linked to maintaining the motor representation as alterations to the motor program occurs through practice (Grafton et al., 1998; Ungerleider et al., 2002). Indeed, recent work by Solopchuk and colleagues (2017) provides evidence of the motor representation of a trained task being held in SMA. Following four days of training on multiple key-press sequences, participants underwent fMRI while performing the trained and untrained (novel) sequences. Prior to undergoing fMRI inhibitory TMS was applied over SMA to permit assessment of the contribution of SMA to both the maintenance and quality of the motor representation as well as performance of the key-press sequences. SMA activation was shown to predict which trained (but not untrained) sequence was executed, indicating that this region held or maintained the sequence specific representation during execution of the task (Solopchuk et al., 2017). In addition, the prediction as to which trained sequence was executed was impaired following inhibitory TMS applied over SMA, thus suggesting that the sequence representation itself was disrupted. As performance of the task itself (untrained or trained sequences) was not impaired, these findings also suggest that the SMA plays a greater role in effector independent vs. dependent encoding. Further support for the role of SMA in effector independent encoding, in the above-mentioned work by Grafton et al. (1998), whereby brain activation was assessed pre/post a single session of sequence learning that involved a transfer of effector groups after training, SMA was shown to be active regardless of the effector (i.e., in contrast to primary motor cortex activation, as stated above).

Further, stemming from findings related to the timing of SMA neuronal output, work suggests that the efference copy, which is sent to the forward model for internal comparisons necessary for updating the motor program as previously mentioned, originates from the SMA (Haggard and Whitford, 2004; Zénon et al., 2015). For instance, disrupting SMA activity via inhibitory TMS in healthy individuals was shown to alter perception of the effort required to perform movement during a task where participants squeezed a dynamometer to varying target force levels (Zénon et al., 2015). Further, Haggard and Whitford (2004) asked participants to judge the intensity of an involuntary finger twitch while performing flexion movements of the index finger at timed and cued intervals. Specifically, two consecutive motor evoked potentials (MEPs) were elicited, whereby the first MEP was preceded with a pre-pulse to the SMA (i.e., to disrupt activity of the SMA in an 'online' manner) on half the trials and the intensity of the second MEP was fixed such that it always resulted in the involuntary finger twitch. The SMA pre-pulse resulted in impaired judgment, thus suggesting that as there was a resulting discrepancy within the forward model, the reafferent signal was not 'cancelled' (Haggard and Whitford, 2004). Collectively, the above work suggests that the efference signal was not sent to the forward model when SMA function was disrupted, thus resulting in an inaccurate prediction of the sensory consequences of the movement.

1.1.7 Motor imagery as a modality of practice

Much of our understanding of motor skill acquisition, and the mechanisms/neural networks underlying motor skill acquisition is derived from studies employing repeated PP of a task; indeed, motor skill acquisition is typically achieved through repeated PP. However, MI is an alternative modality of practice that is employed in a number of domains, including sports, music, and rehabilitation. Evidence abounds of the effectiveness of MI as a modality of motor skill acquisition (Driskell et al., 1994; Jones and Stuth, 1997; Wulf et al., 2010; Schuster et al., 2011; Moran et al., 2012; Brown and Palmer, 2013). For instance, examining findings from 122 studies that employed MI in training (Di Rienzo et al., 2016), MI was shown to faciliate improvements in performance (in terms of both movement accuracy and movement speed). Generally, MI is thought of as an adjunct to PP, whereby it is most effective employed in conjunction or paired with PP (Bovend'eerdt et al., 2012) . Indeed, following six weeks of training of a golf bunker shot, through MI, PP, or combined MI and PP-based practice, the greatest gains in performance were observed after combined MI and PP (Fig. 1.8; Smith et al., 2008). Yet, performance gains from MI-based practice independent of PP have also been shown (Jackson et al., 2003; Zhang et al., 2011; et al., 2012; Malouin et al., 2013) . In the above noted study, MI-based training alone was shown to result in improvements of the bunker shot (Smith et al., 2008). Further, our prior work (Kraeutner et al., 2016b, 2017a) has shown improvements in performance following a single session of MI-based practice of a sequence task whereby the individual does not engage in a physical pre-test (i.e., does not engage in any physical practice or familiarization of the task prior to training). Collectively, the evidence above supports the notion that MI is better than no practice and facilitates motor skill acquisition, supporting its effectiveness as a modality of practice. However, despite this large body of evidence supporting the effectiveness of MI as a form of skill acquisition in a number of domains, we lack critical knowledge related to the underlying mechanism of how skill acquisition is facilitated via this modality of practice. While MI has long been considered analogous to PP but without execution (Jeannerod, 1994, 2001; Decety, 1996; Grèzes and Decety, 2001; Holmes and Collins, 2001; Wakefield et al., 2013), there is evidence that motor skill acquisition via MI-based practice occurs in a fundamentally different way (Kraeutner et al., 2016a, 2017b; Land et al., 2016; Frank and Schack, 2017; Hardwick et al., 2018; Ingram et al., 2019), likely attributed to the lack of sensory feedback during MI. Support for disparate theories of MI are outlined in the following sections below.

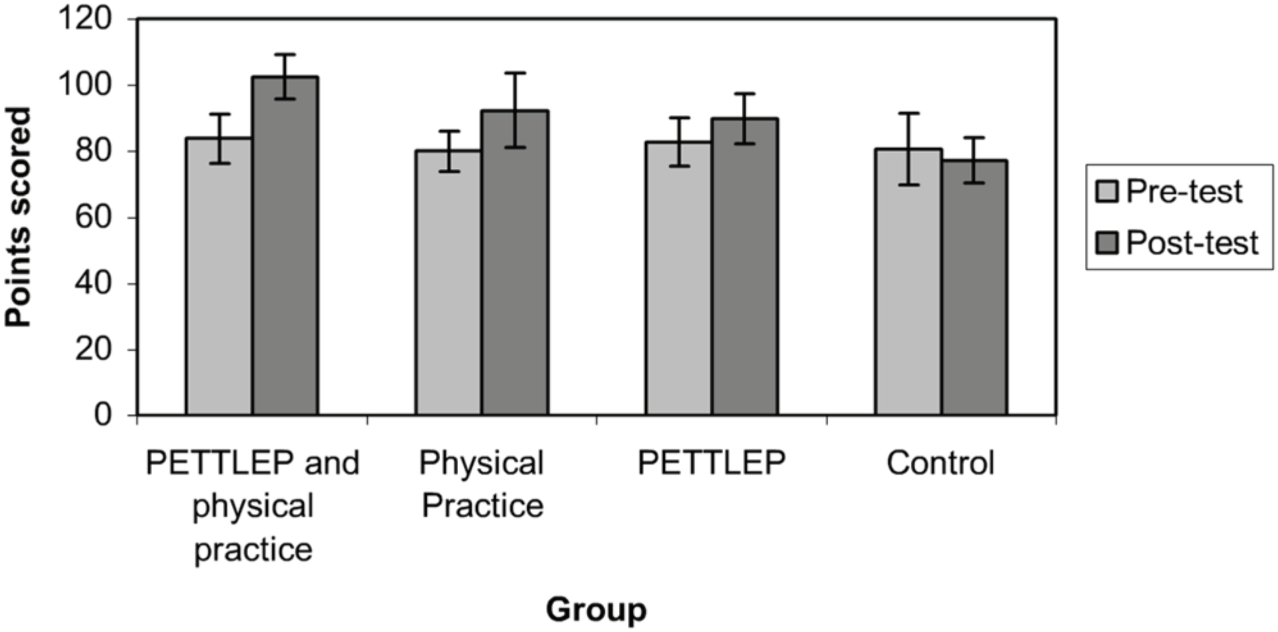


Figure 1.8 Motor imagery (MI) is effective in driving skill acquisition of a golf bunker shot. Following six weeks of training through MI ('PETTLEP'), physical practice (PP), or combined MI and PP, the greatest gains in performance were observed after combined MI and PP. However, improvements in performance were also observed following MI alone, to a similar extent as the PP group.

1.1.8 Functional equivalence of motor imagery

Motor imagery has long been considered analogous to physical practice, in that MI shares underlying mechanisms and neural representations with PP to facilitate a simulation of the movement, referred to as 'the functional equivalence model' (Jeannerod, 1994, 2001; Decety, 1996; Grèzes and Decety, 2001; Holmes and Collins, 2001; Wakefield et al., 2013). Under this model, it is thought that motor skill acquisition via MI is facilitated in the same way as PP – that repetitive imagined practice drives plasticity that ultimately underlies skill acquisition. Specifically, it is thought that MI is an internal simulation of movement, whereby the motor system is required to generate motor images, or that movement-related brain activity is reproduced yet the actual execution is inhibited (Ptak et al., 2017). Thus, both MI and PP rely on the same motor representations that contain movement goals

(Jeannerod, 1994, 1995; Jeannerod and Decety, 1995). Evidence in support of this assumption comes primarily from a large body of neuroimaging work showing similar patterns of brain activity during actual and imagined performance of the same task, albeit at a reduced magnitude during MI (Burianová et al., 2013; Kraeutner et al., 2014; Duann and Chiou, 2016). Specifically, a meta-analysis for neuroimaging investigations of MI demonstrated that MI engages brain regions including the premotor, cingulate, SMA, and parietal cortices (Fig. 1.9; Hétu et al., 2013). As these substrates are critical to learning via PP (Hikosaka et al., 2002; Ungerleider et al., 2002; Doyon and Benali 2005; Dayan and Cohen, 2011), it is thought that MI facilitates motor skill acquisition by driving brain activation in areas critical for skill acquisition (Fig. 1.10; Grèzes and Decety, 2001; Jeannerod, 2001; Holmes and Collins, 2001; Hardwick et al., 2018).

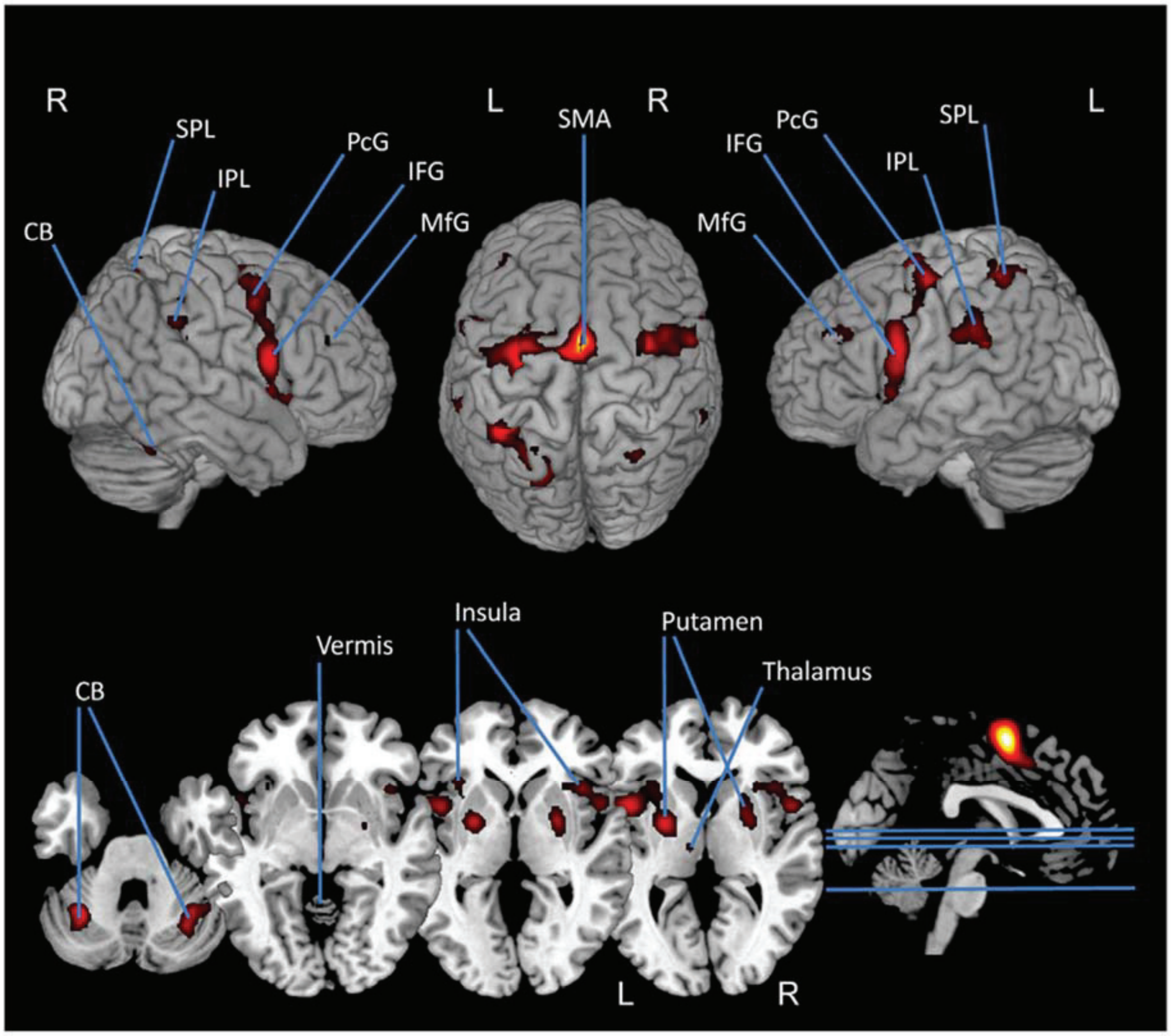


Figure 1.9 Neural correlates of motor imagery, as determined from a meta-analysis for 75 articles that investigated motor imagery-related brain activity of various motor imagery tasks (e.g., sequence tasks, simple explicit motor imagery tasks, and hand laterality judgment tasks) using functional magnetic resonance imaging or positron emission tomography.

Indeed, a large number of investigations employing PET or fMRI comparing activation of the same skill performed through MI or PP in the scanner (often sequence tasks) have determined that both modalities engage many overlapping areas, including premotor, cingulate, and parietal cortices (Porro et al., 1996; Hanakawa et al., 2008; Lange et al., 2008). Studies employing electrophysiological techniques (i.e., electroencephalography (EEG) or magnetoencephalography (MEG) have also been conducted to reveal the neural substrates underlying MI in a more time-sensitive manner (Pfurtscheller and Neuper, 1997; Kawamichi et al., 1998; Neuper et al., 2006; Burianová et al., 2013; Kraeutner et al., 2014). By examining event-related synchronization and desynchronization (ERS/ERD; i.e., an increase or decrease in the magnitude of ongoing cortical oscillations; Pfurtscheller and da Silva, 1999; Pfurtscheller, 2001; Schoffelen and Gross, 2009) to reveal changes in brain activity, it was shown that ERD occurs in contralateral motor areas, primary somatosensory cortex (S1), posterior parietal areas, and cingulate gyri during both MI and PP (Pfurtscheller and Neuper, 1997; Kawamichi et al., 1998; Neuper et al., 2006; Burianová et al., 2013; Kraeutner et al., 2014).

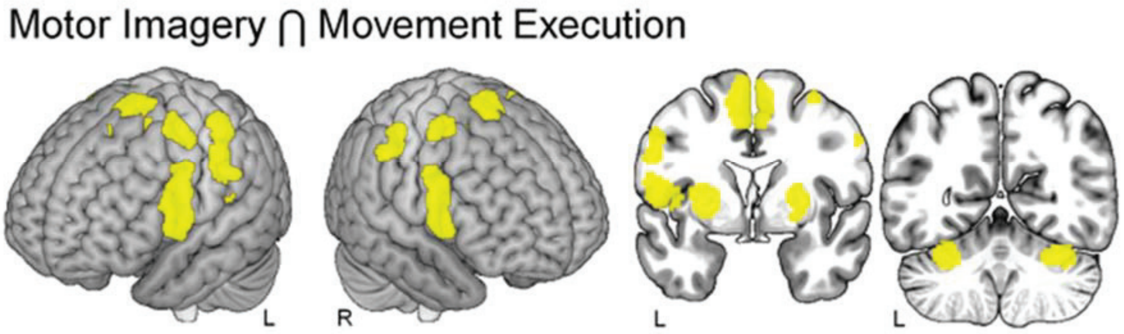


Figure 1.10 Overlapping brain regions during motor imagery and movement execution (i.e., physical practice), as determined via a conjunction analysis across 303 motor imagery-based neuroimaging experiments relative to their physical practice control tasks. Brain regions recruited during both modalities of practice include bilateral inferior parietal lobe, left inferior frontal gyrus, supplementary motor area, and bilateral cerebellum. Adapted from Hardwick et al. (2018).

Under this theory, if MI is functionally equivalent, sharing neural representations with PP, expertise should thus also be reflected in resultant patterns of MI-based brain activation. Indeed, following one week of PP of a sequence task, Lacourse et al. (2005) demonstrated an overlap of brain activation patterns obtained during MI and PP after expertise had been gained. Comparisons conducted to assess brain activation (during PP of the task in the scanner) pre/post a bout of MI-based practice also revealed similar shifts in modality-specific brain activation with motor skill acquisition (Lacourse et al., 2005). Specifically, PP-related brain activity localized to inferior frontal gyrus (IFG), IPL, SMA, and primary motor cortex was shown to decrease following training. Similarly, MI-related brain activity localized to premotor, SMA, and IPL was also shown to decrease following training. Findings from Lacourse et al. (2005) suggest that brain activation associated with refinement of the motor program and consolidation of the skill, linked to improvements in performance, was reflected similarly in resultant patterns of physical and imagined performance of the skill.

In addition, studies examining changes in MI-related brain activation following MI-based training on sequence tasks provides insight on how expertise is achieved through MI. Improvements in performance, measured via response time in a pre/post design, were shown after MI-based practice of a keypress sequence task (14 sessions; Zhang et al., 2011) and foot sequence (five sessions; Jackson et al., 2003). These performance gains associated with increased activity was observed in regions linked to generating or accessing the mental representation of a movement (in particular, cingulate cortex and precuneus; Zhang et al., 2011) and linked to reward- or familiarity-based response selection (namely, orbitofrontal cortex; Elliott et al., 2000; Jackson et al., 2003). However, these studies are limited by the complexity (or lack thereof) of sequence tasks and thus the extent to which conclusions may generalize to complex motor skills is limited (Wulf and Shea, 2002).

Addressing limitations regarding the lack of complexity of a sequence task, neuroimaging studies comparing brain activity between experts (i.e., athletes) and novices (i.e., non-athlete controls) during MI of expert skills provide evidence that brain activity becomes more focal as expertise is gained (Milton et al., 2007; Kim et al., 2008; Chang et al., 2010; Debarnot et al., 2014). For instance, brain activity obtained via fMRI was compared between elite archers and non-archers during MI of an archery task involving six distinct phases of the shot (Chang et al., 2010). Relative to the elite archers, MI in the non-archer group was associated with a bilateral pattern of activity, encompassing primary motor cortex, premotor cortex, IPL, basal ganglia, and cerebellum (Fig. 1.11; Chang et al., 2010). While this work indeed suggests that expertise is reflected in MI-related brain activity, as in PP, these findings are confounded by limitations associated with the nature of between-group designs. Further evidence is thus required to examine how expertise is reflected in MI-related brain activity.

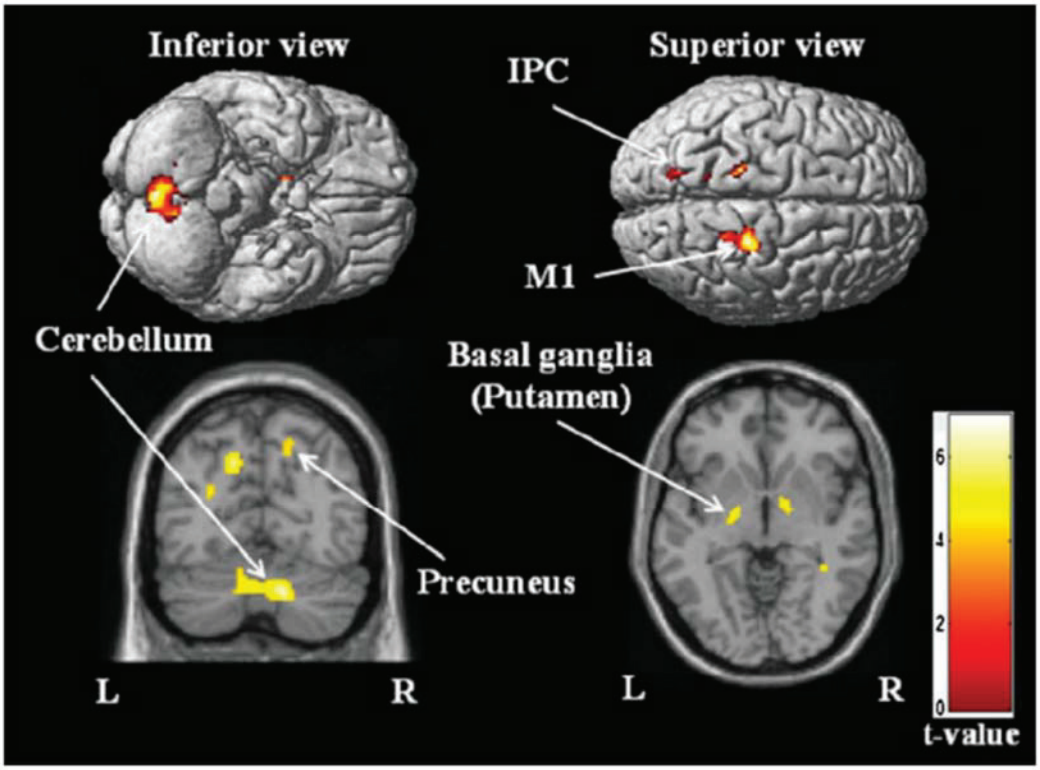


Figure 1.11 Differences in activation shown between novice and elite archers (novice > elite) during motor imagery of an archery shot. Diffuse activation was associated with novice performance: greater activation localized to the primary motor cortex, inferior parietal lobe, basal ganglia and cerebellum was observed for the novice group relative to the elite archers. Taken from Chang et al. (2010).

1.1.9 The nature of MI-based skill acquisition

How the lack of overt execution during MI may impact its mechanism of skill acquisition is also largely unexplored in the literature. Specifically, the entire motor pathway is not activated during MI (i.e., cortical activation is reduced such that descending volleys are insufficient to activate alpha motor neurons in the spinal cord; Grosprêtre et al., 2016, 2018) and the lack of sensory information precludes the ability to rely on feedback to refine the motor program. Thus, whether or not the lack of overt execution (and accompanying sensory feedback) during MI may alter the nature of skill acquisition driven through this modality of practice is discussed below.

In particular, contrary to the functional equivalence model, a growing body of literature suggests that skill acquisition through MI occurs in a fundamentally different way than that which occurs through PP. Specifically, the lack of overt execution during MI may result in differences in the information that is being encoded in MI relative to PP (i.e., primarily effector independent encoding, engendering the abstract representation of the skill; (Annett, 1995; Amemiya et al., 2010; Ingram et al., 2016; Kraeutner et al., 2016a, 2017; Land et al., 2016). Evidence in support of this theory also spans the neuroimaging literature and behavioural investigations of MI. While an overlap of brain activity, as noted above, is demonstrated between MI-based practice and PP (Burianová et al., 2013; Hétu et al., 2013; Kraeutner et al., 2014), MI generally recruits a more diffuse and bilateral network relative to PP (Fig. 1.12; Grézes and Decety, 2001; Burianová et al., 2013; Hétu et al., 2013; Kraeutner et al., 2014; Hardwick et al., 2018). As the contralateral pattern of brain activity typically associated with a unimanual movement reflects an effector-specific pattern of encoding, it is suggested that the bilateral patterns of brain activity observed during MI indicate that the representation has not been mapped to a specific effector (i.e., that only effector independent encoding has occurred; Mizuguchi et al., 2014) Further, these diffuse patterns of brain activity observed during MI include consistent activation of frontal and parietal regions localized to the dorsal stream pathway involved in visuospatial processes (Goodale and Milner, 1992; Rizzolatti and Matelli, 2003; Binkofski and Buxbaum, 2013). For instance, a meta-analysis (Hétu et al., 2013) conducted to determine a general pattern of activation across a number of different MI tasks, including sequences, simple movements, and 'implicit' MI tasks (i.e., whereby the imagery is thought to occur without conscious awareness) revealed consistent activation in regions including the IPL, SPL, IFG, middle frontal gyri (MFG), and SMA (Hétu et al., 2013). Further, activation in primary motor cortex during MI is known to be inconsistent (Burianová et al., 2013; Hétu et al., 2013; Kraeutner et al., 2014), thus suggesting that this region does not play a critical role in MI. Further, in a meta-analysis where contrast analyses were conducted between 303 MI-related neuroimaging experiments and embedded PP conditions, more consistent activation localized to premotor and parietal regions was associated with MI vs. PP (Fig. 1.13; Hardwick et al., 2018). Interestingtly as effector independent encoding is thought to be supported by a parietal-frontal circuit, in contrast to effector dependent encoding primarily supported by core motor regions (namely, primary motor cortex and premotor areas; Grafton et al. 1998; Hikosaka et al., 2002; Bapi et al., 2006; Gallivan et al., 2011), further support is provided for the effector independent nature of MI.

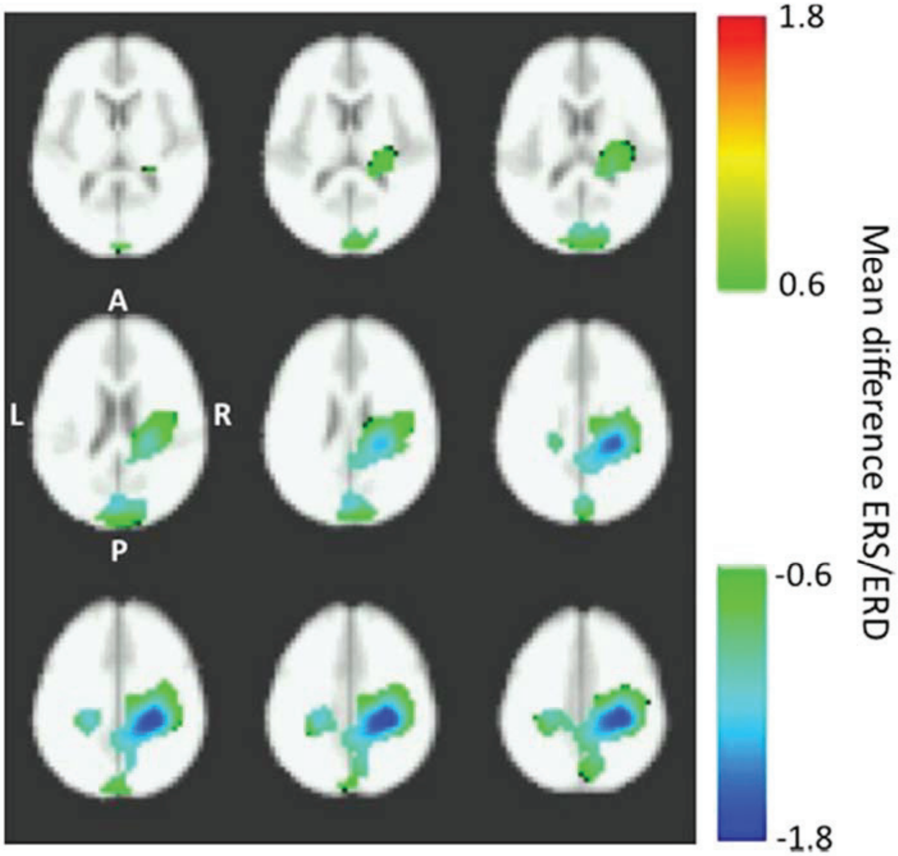


Figure 1.12 Differences in activation ("ERS/ERD"; reflecting the power change of oscillatory activity in the beta band over time) shown between physical practice and motor imagery of a unimanual sequence task. Areas of significant differences in activation ($p < 0.05$) were determined from 3d t-tests of physical practice vs. imagery blocks. More lateralized activation was associated with physical practice: greater activation within the contralateral hemisphere, localized to primary motor cortex and somatosensory cortex, was observed during physical practice relative to motor imagery. Taken from Kraeutner et al. (2014).

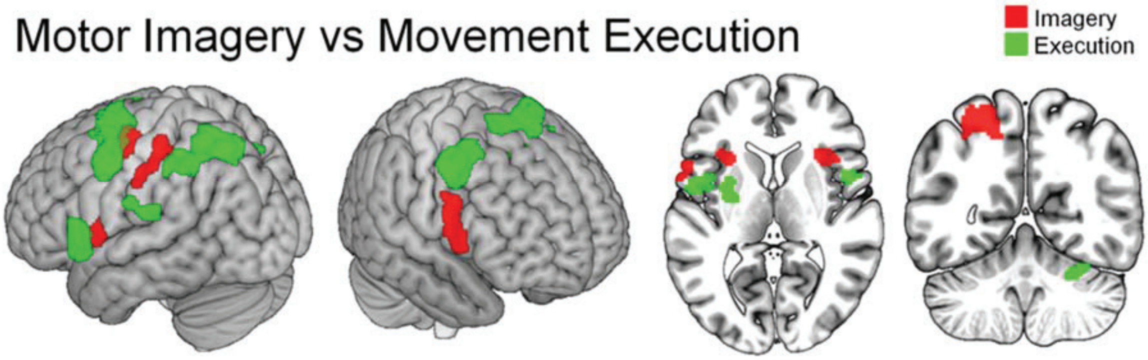


Figure 1.13 Differences in activation shown between physical practice ('movement execution'), determined via a contrast analysis across 303 motor imagery-based neuroimaging experiments and embedded physical practice control conditions. Classic sensorimotor regions were more consistently activated during physical practice relative to motor imagery: motor imagery was more consistently associated with activation localized to premotor and posterior parietal regions (including left inferior and superior parietal lobes). Physical practice was more consistently associated with activation localized to supplementary motor area, left primary motor cortex, somatosensory cortex, putamen, and the right cerebellum (lobule VI). Adapted from Hardwick et al. (2018).

While the above neuroimaging studies do not provide causal evidence, the effector independent nature is likely best illustrated by lesion studies and work emplyoing inhibitory non-invasive brain stimuation to posterior parietal regions implicated in effector independent encoding (namely, the IPL) during MI (Sirigu et al., 1996; Evans et al., 2016; Kraeutner et al., 2016a; McInnes et al., 2016; Oostra et al., 2016). For instance, performance on implicit MI tasks (in which the participant performs MI, activating motororic pathways, without conscious awareness to solve a spatial orientation problem typically involving hands) is impaired following inhbitory stimulation to the left IPL (Evans et al., 2016; Kraeutner et al., 2019): Evans et al. (2016) showed a decrease in performance both in patients with left IPL lesions and in neurotypical participants following inhibition to the left IPL via transcranial direct current stimulation (tDCS) during a perceptual decision-making task in which participants were required to identify the correct hand posture for target objects (e.g., a key, or a hammer), Kraeutner et al. (2019)

showed a decrease in performance in healthy participants following inhibition to the left IPL via TMS during the hand laterality judgment task, where participants were to determine whether or not a hand present on a screen is a left or right hand.

Further, inhibition of the left IPL via TMS was shown to abolish improvements in performance following MI-based practice of a sequence learning task (Fig. 1.14; Kraeutner et al., 2016a). Of note, inhibition of the left IPL did not impair the actual execution component (i.e., key-press response), and the authors concluded that the ability to perform MI, and in turn learn the sequence through MI, was impaired. Using this same task however, inhibition of either left or right primary motor cortex did not affect the learning that occurred through MI (i.e., learning occurred to a similar extent between groups undergoing motor cortex stimulation and both control and sham stimulation groups; Fig. 1.14; Kraeutner et al., 2017b). Taken together, these findings speak directly to the inherent differences between MI and PP, as prior work has shown that inhibition of primary motor cortex impairs skill acquisition via PP in a similar sequence tasks (Rosenthal et al., 2010; Steel et al., 2016).

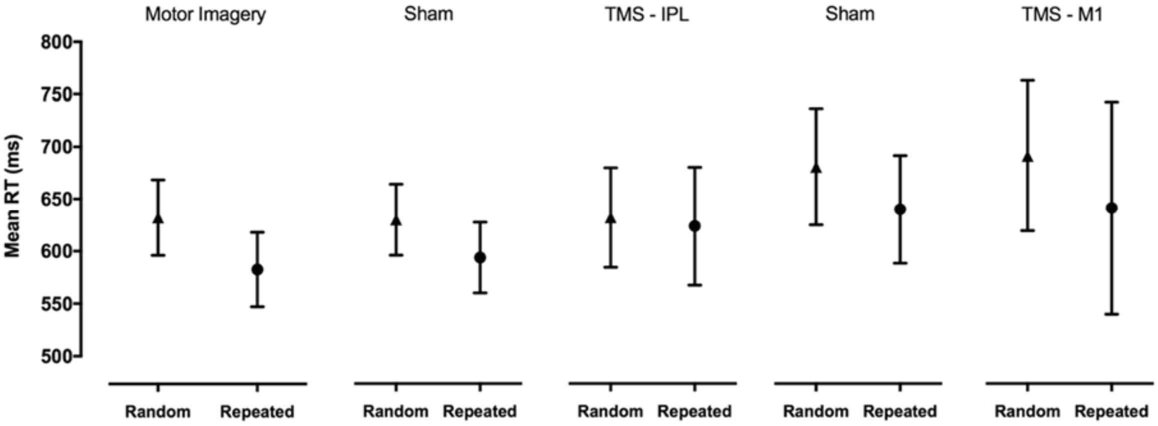


Figure 1.14 Improvements in performance following MI-based practice of a sequence task are abolished after inhibitory stimulation to the inferior parietal lobe ('TMS-IPL') but not the primary motor cortices ('TMS-M1'), as determined by comparing reaction times to trained ('Repeated') vs. untrained ('Random') sequences. Adapted from Kraeutner et al. (2016a; 2017b).

Interestingly, work employing transfer tasks after a bout of MI or PP-based training also suggests that MI and PP are fundamentally different. In particular, as per the functional equivalence model, that MI and PP share neural representations and mechanisms indicates that performance on transfer task should be similar. On the contrary, Land et al. (2016) employed a motor transfer task in which participants practiced a key-press sequence for forty minutes with one hand via MI or PP, and were then asked to engage in a test block where they performed the sequence with the trained and untrained hand. Greater performance was observed following PP for the trained vs. untrained hand (as expected). PP also led to greater performance with the trained hand, relative to MI. However, PP did not show an advantage over MI on the untrained hand, and MI-based practice resulted in similar improvements in performance between both the trained and untrained hand. Therefore, the information encoded (e.g., spatial sequence learning) during MI-based practice training was not mapped to a specific effector (i.e., was equally shared by both the trained and untrained limbs). In employing a sequence-learning paradigm, Ingram et al.

(2016) also demonstrated that a perceptual transfer task disrupted MI-based learning greater than PP-based learning, yet the opposite was observed during a motor transfer task (i.e., PP-based learning was disrupted greater than MI-based learning). The authors thus concluded that MI relies on mapping perceptual cues to movement goals, but that MI may not encode information specific to an effector (Ingram et al., 2016).

Importantly, the absence of sensory information precludes the use of feedback in internal comparisons to update the motor program. However, an alternative error detection/correction mechanism may be at work to update the motor program, as MI is thought to still rely on a forward model (Fig. 1.15; Kilteni et al., 2018; Dahm and Rieger, 2019; Ingram et al., 2019). Indeed, prior work suggests that the motor program undergoes training-related alterations during MI-based practice (Gentili et al., 2006, 2010; Kraeutner et al., 2016b; Ingram et al., 2019). For instance, in employing a multi-articular tracing task over 5 sessions, Ingram and colleagues (2019) showed that MI-based practice facilitated improvements in performance that while smaller in magnitude relative to PP, were greater than that observed for PP without visual feedback (Ingram et al., 2019). The authors posited that MI-based learning does not depend on sensory feedback and instead occurs through an alternative mechanism where feedback is simulated. Supported by the aforementioned neuroimaging evidence, highlighting SMA and cerebellar activity during MI – key regions that support the error/detection and forward model comparisons – it is suggested that the predicted consequences of the movement are compared to a simulated representation of the movement that produces a corresponding sensory representation (O'Shea and Moran, 2017; Kilteni et al., 2018; Ingram et al., 2019). However, given that MI led to smaller improvements in performance than PP (Ingram et al., 2019), it is likely that any discrepancy observed between the predicted consequences and simulated feedback representation is much smaller (or the quality of the motor prediction is reduced in the absence of sensory information; Gentili et al., 2006) than that which occurs when feedback is derived from actual sensory information. Consequently, smaller updates are made to the motor program (Ingram et al., 2019).

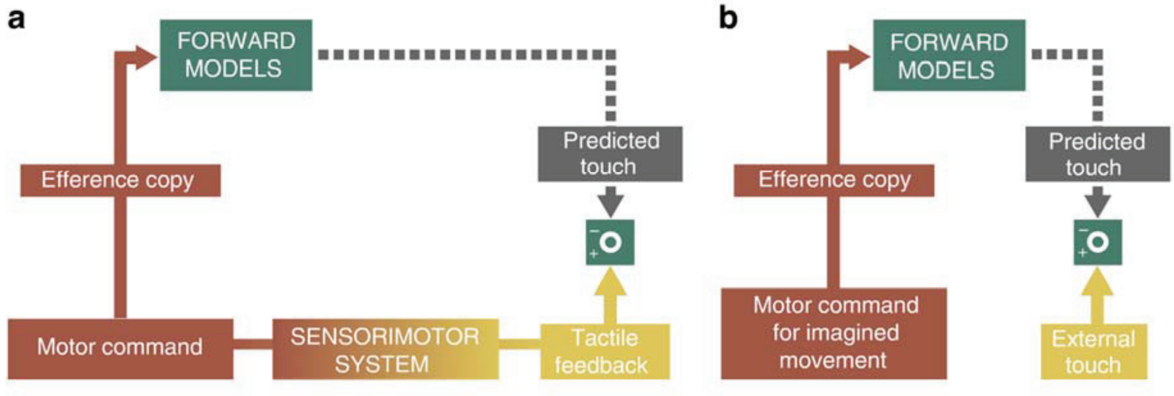


Figure 1.15 Illustration of somatosensory attenuation observed during a) a self-generated touch (i.e., pressing one index finger against the other). As the forward models predict the associated sensory consequences, including the tactile feedback from the self-touch, the predicted touch attenuates the actual sensory feedback. And, b) motor imagery of a self-generated touch. When an external stimulus is applied providing matching tactile feedback, the perceived intensity is reduced, indicating that it has already been predicted by the forward model as during actual execution of the touch. Thus, forward models are thought to predict the associated consequences of a movement during motor imagery. Taken from Kilteni et al. (2018).

Relative to the body of literature related to the mechanisms of PP, we lack fundamental knowledge related to how the lack of sensory information, and/or the effector independent nature of MI drives skill acquisition. In the context of the aforementioned framework provided by Fitts and Posner (1967), the reliance of MI on effector independent encoding may ultimately facilitate the cognitive (and perhaps associative) but not autonomous stage of motor skill acquisition. Thus, MI would be rendered ineffective in later stages of motor skill acquisition, once the motor program has been consolidated. Yet, in relying to a greater extent on cognitive processes, or processes linked to effector independent encoding, MI may drive more elaborate representations of the skill, and in turn more flexible learning relative to PP (Frank et al., 2014; Frank et al., 2015; Land et al., 2016; Frank and Schack, 2017). In this scenario, MI would be more effective in the early stages of motor skill acquisition, as the individual learns the task goals and movement elements. Further, the encoding driven via MI may act as scaffolding, for which greater gains in performance can be readily facilitated through PP.

Interestingly, work from Frank and others (Frank et al., 2014, 2015; Frank and Schack, 2017; Kim et al., 2017), has shown that skill acquisition through MI promotes the development of a more elaborate abstract representation of the movement relative to PP. Specifically, the development of movement representations on a golf putting task was examined following three days of MI-based practice, PP, combined MI and PP, and no practice (Frank et al., 2014). To examine changes in how the representation of a movement/skill changes over the course of motor skill acquisition, a previously established analysis was applied whereby the mental representation for a complex skill is thought to be comprised of a number of different movement ‘chunks’ (termed basic action concepts) that are organized into a hierarchical structure as expertise is gained (outlined in Schack, 2004; Schack and Mechsner, 2006; Frank et al., 2013). Thus, assessing the extent to which the chunks are structurally organized informs on the richness or elaborateness of the representation (Schack, 2004; Schack and Mechsner, 2006; Frank et al., 2013; 2014). Interestingly, in the aforementioned study, combined MI and PP led to the greatest changes and the most elaborate representations (Frank et al., 2014). Yet, MI vs. PP led to more structured and elaborate representations (Frank et al., 2014). Regarding performance outcomes however, MI-based practice resulted in limited improvements relative to PP, and combined MI and PP did not lead to superior putting performance relative to PP alone. This body of work suggests that MI facilitates motor skill acquisition in the early (i.e., the cognitive) stage, by driving perceptual-cognitive changes necessary to refine the representation of the movement, yet does not manifest in robust behavioural changes at the motor output level (i.e., the movement plan is not mapped to the effector or no effector dependent encoding occurs; Frank et al., 2014, 2015; Frank and Schack, 2017; Kim et al., 2017). However, how these theories translate to neural and behavioural outcomes observed across longitudinal (training) studies is unexplored.

1.2 OVERVIEW OF THESIS CHAPTERS

The overarching objective of this thesis is to provide new knowledge related to the neural mechanisms of MI and the nature of MI-based skill acquisition. This objective has been approached in a number of different ways: a cross-sectional study to determine that expertise is reflected in MI-related brain activation (Chapter 2), a longitudinal study to examine pre/post changes in how the modality in which expertise is gained manifests as differences in behaviour and resultant patterns of brain activation (Chapter 3), and a longitudinal crossover study that assessed brain activation and performance at multiple time points to probe the way in which MI facilitates skill acquisition (Chapter 4). Chapters 1 and 5, which presents a general discussion of the main findings of the thesis and limitations, were written by Sarah Kraeutner, with Dr. Boe providing editorial assistance. Chapters 2-4 comprise original research, and each experiment addressed a relevant question pertaining to the mechanisms underlying MI that had not been previously considered in the motor skill acquisition literature.

Chapter 2 is based on work conducted by Sarah Kraeutner, Jack Solomon, Dr. Sean McWhinney, Dr. Lori Dithurbide, and Dr. Shaun Boe. Sarah Kraeutner was responsible for study conception, data collection, analyses and interpretation, and writing and revising the manuscript. Jack Solomon and Dr. Lori Dithurbide assisted in study design and revising the manuscript. Dr. Sean McWhinney assisted in data analyses and revising the manuscript. Dr. Shaun Boe assisted in study design and editing the manuscript.

Chapter 3 is based on work conducted by Sarah Kraeutner, Alexandra Stratas, Jennifer McArthur, Carl Helmick, and Drs. David Westwood and Shaun Boe. Sarah Kraeutner, Dr. David Westwood, and Dr. Shaun Boe conceived the study. Sarah Kraeutner was responsible for data collection, with assistance from Alexandra Stratas and Jennifer McArthur. Sarah Kraeutner was responsible for data analyses, with assistance from Alexandra Stratas, Jennifer McArthur, and Carl Helmick. Sarah Kraeutner interpreted the data, and wrote and revised the manuscript in consultation with Dr. Shaun Boe. Dr. David Westwood provided edits to the final version(s) of the manuscript.

Chapter 4 is based on work conducted by Sarah Kraeutner, Alexandra Stratas, Jennifer McArthur, and Drs. Paul Kraeutner, David Westwood, and Shaun Boe. Sarah Kraeutner conceived the study with Drs. David Westwood and Shaun Boe. Sarah Kraeutner was responsible for data collection with assistance from Alexandra Stratas and Jennifer McArthur. Sarah Kraeutner was responsible for data analyses, with assistance from Jennifer McArthur and Dr. Paul Kraeutner. Sarah Kraeutner was responsible for interpreting the data with assistance from Drs. Paul Kraeutner and Shaun Boe. Sarah Kraeutner wrote and revised the manuscript in consultation with Dr. Shaun Boe. Dr. David Westwood provided edits to the final version(s) of the manuscript. Collectively, this work provides new knowledge related to the mechanism of how motor skill acquisition occurs via MI, and informs on the application of MI as a modality of practice.

1.2.1 Specific aims and hypotheses for each chapter

Chapter 2 aims: To determine how expertise modulates brain activity driven via MI, through examining 1) within-group differences in brain activity of experts (i.e., varsity athletes) performing MI of a sport-specific task vs. a novel task, and 2) differences in brain activity between experts and recreational controls during MI of a task that all groups have a similar degree of expertise of, so as to control for task-driven differences in the within-group comparisons.

Chapter 2 hypotheses: First, that within-group comparisons of MI-related brain activity would reveal bilateral and diffuse patterns of brain activation, including increased recruitment of bilateral frontal and parietal regions critical to visuospatial processes, associated with the novel vs. expert task. Second, that between-group comparisons would reveal no differences in brain activation patterns of tasks for which participants had similar expertise of.

Chapter 3 aims: Building on work conducted in Chapter 2, as expertise was gained primarily through PP and no conclusions can be drawn in regard to the extent to which practice modality contributed to the achieved level of expertise (or the extent to which MI was used to facilitate learning is unknown), Chapter 3 sought to determine how expertise of a complex motor skill evolves when the expertise is achieved via MI relative to PP. To achieve this objective, brain activation and performance outcomes were directly compared before and after five days of training of a complex motor skill via PP or MI.

Chapter 3 hypotheses: We hypothesized that cerebellar and contralateral regions within the motor network, would show increased activation following MI-based training, albeit at a reduced magnitude relative to PP. Further, that performance would improve would improve following MI-based training, with the degree of these improvements inferior to those observed following PP-based training.

Chapter 4 aims: Building on work conducted in Chapter 3 and established differences of brain activation noted in the literature between MI and PP of the same task, whereby noted disparities in resultant patterns of brain activation and performance outcomes between the two practice modalities led to the notion that information encoded during MI lends itself to the early stage of learning, Chapter 4 sought to examine the nature of MI-based skill acquisition by manipulating the order of MI and PP in training of a complex motor skill. Specifically, the prediction that the nature of MI lends itself to facilitating encoding of effector independent representations, critical to the early stage of learning, was tested by comparing improvements in performance and changes in brain activation when MI was applied either prior to, or after PP-based training.

Chapter 4 hypotheses: Given an equal dose of MI and PP, it is hypothesized that the greatest gains in performance of a motor skill would be observed when MI-based training preceded PP-based training (as opposed to when MI follows PP). Further, that regardless of where MI was applied, changes in performance driven by MI would manifest only as improvements in global vs. specific performance outcomes. Finally, that robust changes in brain activation within the sensorimotor network would solely be induced by PP.

1.3 REFERENCES

Amemiya K, Ishizu T, Ayabe T, Kojima S (2010) Effects of motor imagery on intermanual transfer: a near-infrared spectroscopy and behavioural study. Brain research 1343:93–103.

Annett J (1995) Motor imagery: perception or action? Neuropsychologia 33:1395–1417.

Apolinário-Souza T, Romano-Silva MA, de Miranda DMM, Malloy-Diniz LF, Benda RN, Ugrinowitsch H, Lage GM (2016) The primary motor cortex is associated with learning the absolute, but not relative, timing dimension of a task: A tDCS study. Physiol Behav 160:18–25.

Ashe J, Georgopoulos A (1994) Movement parameters and neural activity in motor cortex and area 5. Cerebral Cortex 4:590–600.

Bapi RS, Doya K, Harner AM (2000) Evidence for effector independent and dependent representations and their differential time course of acquisition during motor sequence learning. Exp Brain Res 132:149–162.

Bapi RS, Miyapuram KP, Graydon FX, Doya K (2006) fMRI investigation of cortical and subcortical networks in the learning of abstract and effector-specific representations of motor sequences. Neuroimage 32:714–727.

Bastian AJ (2006) Learning to predict the future: the cerebellum adapts feedforward movement control. Current opinion in neurobiology Available at: http://www.sciencedirect.com/science/article/pii/S0959438806001395.

Binkofski F, Buxbaum LJ (2013) Two action systems in the human brain. Brain Lang 127:222–229.

Blakemore S-J, Sirigu A (2003) Action prediction in the cerebellum and in the parietal lobe. Experimental Brain Research 153:239–245 Available at: http://link.springer.com/article/10.1007/s00221-003-1597-z.

Blakemore SJ, Wolpert DM, Frith CD (1998) Central cancellation of self-produced tickle sensation. Nat Neurosci 1:635–640.

Boe SG, Cassidy RJ, McIlroy WE, Graham SJ (2012) Single session motor learning demonstrated using a visuomotor task: Evidence from fMRI and behavioural analysis. J Neurosci Methods 209:308–319.

Bovend'eerdt TJ, Dawes H, Sackley C, Wade DT (2012) Practical research-based guidance for motor imagery practice in neurorehabilitation. Disabil Rehabil 34:2192–2200.

Brooks JX, Cullen KE (2013) The Primate Cerebellum Selectively Encodes Unexpected Self-Motion. Curr Biol 23:947–955.

Brown RM, Palmer C (2013) Auditory and motor imagery modulate learning in music performance. Frontiers in Human Neuroscience 7:1–13.

Burianová H, Marstaller L, Sowman P, Tesan G, Rich A, Williams M, Savage G, Johnson B (2013) Multimodal functional imaging of motor imagery using a novel paradigm. NeuroImage 71:50–58.

Buxbaum, Johnson-Frey, Bartlett-Williams (2005) Deficient internal models for planning hand–object interactions in apraxia.

Buxbaum LJ, Kyle K, Grossman M, Coslett HB (2007) Left inferior parietal representations for skilled hand-object interactions: evidence from stroke and corticobasal degeneration. Cortex 43:411–423.

Buxbaum LJ, Kyle KM, Tang K, Detre JA (2006) Neural substrates of knowledge of hand postures for object grasping and functional object use: evidence from fMRI. Brain Res 1117:175–185.

Chang Y, Lee J-J, Seo J-H, Song H-J, Kim Y-T, Lee H, Kim H, Lee J, Kim W, Woo M, Kim J (2010) Neural correlates of motor imagery for elite archers. NMR in Biomedicine 24:366-72.

Cowper-Smith C, Lau E, Helmick C, Eskes G, Westwood D (2010) Neural Coding of Movement Direction in the Healthy Human Brain. Plos One 5:e13330.

Cunnington R, Windischberger C, Deecke L, Moser E (2003) The preparation and readiness for voluntary movement: a high-field event-related fMRI study of the Bereitschafts-BOLD response. Neuroimage 20:404–412.

Cunnington R, Windischberger C, Moser E (2005) Premovement activity of the pre-supplementary motor area and the readiness for action: Studies of time-resolved event-related functional MRI. Human Movement Science 24:644–656.

Dahm S, Rieger M (2019) Is imagery better than reality? Performance in imagined dart throwing. Hum Movement Sci 66:38–52.

Dayan E, Cohen LG (2011) Neuroplasticity subserving motor skill learning. Neuron 72:443–454.

Debarnot U, Sperduti M, Di Rienzo F, Guillot A (2014) Experts bodies, experts minds: How physical and mental training shape the brain. Front Hum Neurosci 8:280.

Decety J (1996) Do imagined and executed actions share the same neural substrate? Brain Res Cogn Brain Res 3:87–93.

Deecke L, Kornhuber H (1978) An electrical sign of participation of the mesial “supplementary” motor cortex in human voluntary finger movement. Brain Res 159:473–476.

Di Rienzo F, Debarnot U, Daligault S, Saruco E, Delpuech C, Doyon J, Collet C, Guillot A (2016) Online and Offline Performance Gains Following Motor Imagery Practice: A Comprehensive Review of Behavioral and Neuroimaging Studies. Front Hum Neurosci 10:315.

Doyon J, Benali H (2005) Reorganization and plasticity in the adult brain during learning of motor skills. Curr Opin Neurobiol 15:161–167.

Doyon J, Song A, Karni A, Lalonde F, Adams M, Ungerleider L (2002) Experience-dependent changes in cerebellar contributions to motor sequence learning. Proc National Acad Sci 99:1017–1022.

Driskell J, Copper C, Moran A (1994) Does mental practice enhance performance? Journal of Applied Psychology 79:481.

Duann J-RR, Chiou J-CC (2016) A Comparison of Independent Event-Related Desynchronization Responses in Motor-Related Brain Areas to Movement Execution, Movement Imagery, and Movement Observation. PLoS ONE 11:e0162546.

Elliott R, Dolan RJ, Frith CD (2000) Dissociable functions in the medial and lateral orbitofrontal cortex: evidence from human neuroimaging studies. Cereb Cortex 10:308–317.

Espinoza E, Smith AM (1990) Purkinje cell simple spike activity during grasping and lifting objects of different textures and weights. J Neurophysiol 64:698–714.

Evans C, Edwards MG, Taylor LJ, Ietswaart M (2016) Perceptual decisions regarding object manipulation are selectively impaired in apraxia or when tDCS is applied over the left IPL. Neuropsychologia 86:153–166.

Fitts, P. M., Posner, M. I. (1967). Human performance. Belmont, CA: Brooks/Cole.

Flash T, Bizzi E (2016) Cortical circuits and modules in movement generation: experiments and theories. Curr Opin Neurobiol 41:174–178.

Floyer-Lea A, Matthews PM (2005) Distinguishable brain activation networks for short- and long-term motor skill learning. J Neurophysiol 94:512–518.

Frank C, Land W, Schack T (2013) Mental representation and learning: The influence of practice on the development of mental representation structure in complex action. Psychol Sport Exerc 14:353–361.

Frank C, Land WM, Popp C, Schack T (2014) Mental representation and mental practice: experimental investigation on the functional links between motor memory and motor imagery. PLoS ONE 9:e95175.

Frank C, Land WM, Schack T (2015) Perceptual-Cognitive Changes During Motor Learning: The Influence of Mental and Physical Practice on Mental Representation, Gaze Behavior, and Performance of a Complex Action. Front Psychol 6:1981.

Frank C, Schack T (2017) The Representation of Motor (Inter)action, States of Action, and Learning: Three Perspectives on Motor Learning by Way of Imagery and Execution. Front Psychol 8:678.

Gallivan JP, McLean DA, Smith FW, Culham JC (2011) Decoding effector-dependent and effector-independent movement intentions from human parieto-frontal brain activity. J Neurosci 31:17149–17168.

Gao JH, Parsons LM, Bower JM, Xiong J, Li J, Fox PT (1996) Cerebellum implicated in sensory acquisition and discrimination rather than motor control. Science 272:545–547.

Gentili R, Han CE, Schweighofer N, Papaxanthis C (2010) Motor learning without doing: trial-by-trial improvement in motor performance during mental training. J Neurophysiol 104:774–783.

Gentili R, Papaxanthis C, Pozzo T (2006) Improvement and generalization of arm motor performance through motor imagery practice. Neuroscience 137:761–772.

Georgopoulos AP (1990) Neural coding of the direction of reaching and a comparison with saccadic eye movements. Cold Spring Harb Symp Quant Biol 55:849–859.

Georgopoulos, Schwartz, Kettner (1986) Neuronal population coding of movement direction. Science 233:1416–1419.

Goodale MA, Milner AD (1992) Separate visual pathways for perception and action. Trends Neurosci 15:20–25.

Goodale MA, Westwood DA (2004) An evolving view of duplex vision: separate but interacting cortical pathways for perception and action. Curr Opin Neurobiol 14:203–211.

Grafton, Hazeltine, Ivry (2002) Motor sequence learning with the nondominant left handA PET functional imaging study.

Grafton ST, Hazeltine E, Ivry RB (1998) Abstract and effector-specific representations of motor sequences identified with PET. J Neurosci 18:9420–9428.

Grafton S, Mazziotta J, Presty S, Friston K, Frackowiak R, Phelps M (1992) Functional anatomy of human procedural learning determined with regional cerebral blood flow and PET. J Neurosci 12:2542–2548.

Grèzes J, Decety J (2001) Functional anatomy of execution, mental simulation, observation, and verb generation of actions: a meta-analysis. Hum Brain Mapp 12:1–19.

Grosprêtre S, Lebon F, Papaxanthis C, Martin A (2016) New evidence of corticospinal network modulation induced by motor imagery. J Neurophysiol 115:1279–1288.

Grosprêtre S, Lebon F, Papaxanthis C, Martin A (2018) Spinal plasticity with motor imagery practice. J Physiol (Lond).

Haggard P, Whitford B (2004) Supplementary motor area provides an efferent signal for sensory suppression. Cognitive Brain Res 19:52–58.

Hanakawa T, Dimyan M, Hallett M (2008) Motor Planning, Imagery, and Execution in the Distributed Motor Network: A Time-Course Study with Functional MRI. Cerebral Cortex 18:2775–2788.

Hardwick R, Rottschy C, Miall R, Eickhoff S (2013) A quantitative meta-analysis and review of motor learning in the human brain. NeuroImage 67:283–297.

Hardwick RM, Caspers S, Eickhoff SB, Swinnen SP (2018) Neural correlates of action: Comparing meta-analyses of imagery, observation, and execution. Neurosci Biobehav Rev 94:31–44.

Hétu S, Grégoire M, Saimpont A, Coll M-P, Eugène F, Michon P-E, Jackson P (2013) The neural network of motor imagery: An ALE meta-analysis. Neuroscience and biobehavioral reviews 37:930–949.

Hikosaka O, Nakamura K, Sakai K, Nakahara H (2002) Central mechanisms of motor skill learning. Curr Opin Neurobiol 12:217–222.

Holmes P, Collins D (2001) The PETTLEP Approach to Motor Imagery: A Functional Equivalence Model for Sport Psychologists. J Appl Sport Psychol 13:60–83.

Ingram TG, Kraeutner SN, Solomon JP, Westwood DA, Boe SG (2016) Skill acquisition via motor imagery relies on both motor and perceptual learning. Behav Neurosci 130:252–260.

Ingram TGJG, Solomon JP, Westwood DA, Boe SG (2019) Movement related sensory feedback is not necessary for learning to execute a motor skill. Behav Brain Res 359:135–142.

Jackson P, Lafleur M, Malouin F, Richards C, Doyon J (2003) Functional cerebral reorganization following motor sequence learning through mental practice with motor imagery. NeuroImage 20:1171–1180.

Jeannerod M (1994) The representing brain: Neural correlates of motor intention and imagery. Behavioral and Brain Sciences 17:187–245.

Jeannerod M (1995) Mental imagery in the motor context. Neuropsychologia 33:1419–1432.

Jeannerod M (2001) Neural Simulation of Action: A Unifying Mechanism for Motor Cognition. NeuroImage 14:S103–S109.

Jeannerod M, Decety J (1995) Mental motor imagery: a window into the representational stages of action. Curr Opin Neurobiol 5:727–732.

Jenkins I, Brooks D, Nixon P, Frackowiak R, Passingham R (1994) Motor sequence learning: a study with positron emission tomography. J Neurosci 14:3775–3790.

Jones L, Stuth G (1997) The uses of mental imagery in athletics: An overview. Applied and Preventive Psychology.

Jueptner M, Ottinger S, Fellows SJ, Adamschewski J, Flerich L, Müller SP, Diener HC, Thilmann AF, Weiller C (1997) The Relevance of Sensory Input for the Cerebellar Control of Movements. Neuroimage 5:41–48.

Kandel, E. R., Schwartz, J. H., Jessell, T. M. (2000). Principles of neural science (4th ed.). NEW YORK: McGraw-Hill, Health Professions Division.

Karni A, Meyer G, Rey-Hipolito C, Jezzard P, Adams MM, Turner R, Ungerleider LG (1998) The acquisition of skilled motor performance: fast and slow experience-driven changes in primary motor cortex. Proc Natl Acad Sci USA 95:861–868.

Kawamichi H, Kikuchi Y, Endo H, Takeda T, Yoshizawa S (1998) Temporal structure of implicit motor imagery in visual hand-shape discrimination as revealed by MEG. Neuroreport 9:1127–1132.

Kilteni K, Andersson BJ, Houborg C, Ehrsson HH (2018) Motor imagery involves predicting the sensory consequences of the imagined movement. Nat Commun 9:187.

Kim J, Lee H, Kim W, Park H, Kim S, Moon D, Woo M, Tennant L (2008) Neural correlates of pre-performance routines in expert and novice archers. Neurosci Lett 445:236–241.

Kim T, Frank C, Schack T (2017) A Systematic Investigation of the Effect of Action Observation Training and Motor Imagery Training on the Development of Mental Representation Structure and Skill Performance. Front Hum Neurosci 11:499.

Kraeutner S, Gionfriddo A, Bardouille T, Boe S (2014) Motor imagery-based brain activity parallels that of motor execution: Evidence from magnetic source imaging of cortical oscillations. Brain research 1588:81–91.

Kraeutner SN, El-Serafi M, Lee J, Boe SG (2019) Disruption of motor imagery performance following inhibition of the left inferior parietal lobe. Neuropsychologia 127:106-112.

Kraeutner SN, Gaughan TC, Eppler SN, Boe SG (2017a) Motor imagery-based implicit sequence learning depends on the formation of stimulus response associations. Acta Pscyhologica 31:48–55.

Kraeutner SN, Ingram TGJG, Boe SG (2017b) The effector independent nature of motor imagery: Evidence from rTMS induced inhibition to the primary motor cortices. Neuropsychologia 97:1–8.

Kraeutner SN, Keeler LT, Boe SG (2016a) Motor imagery-based skill acquisition disrupted following rTMS of the inferior parietal lobule. Experimental brain research 234:397–407.

Kraeutner SN, MacKenzie LA, Westwood DA, Boe SG (2016b) Characterizing skill acquisition through motor imagery with no prior physical practice. Journal of experimental psychology Human perception and performance 42:257–265.

Lacourse MG, Orr EL, Cramer SC, Cohen MJ (2005) Brain activation during execution and motor imagery of novel and skilled sequential hand movements. Neuroimage 27:505–519.

Lacourse MG, Turner JA, Randolph-Orr E, Schandler SL, Cohen MJ (2004) Cerebral and cerebellar sensorimotor plasticity following motor imagery-based mental practice of a sequential movement. J Rehabil Res Dev 41:505–524.

Land WM, Liu B, Cordova A, Fang M, Huang Y, Yao WX (2016) Effects of Physical Practice and Imagery Practice on Bilateral Transfer in Learning a Sequential Tapping Task. PLoS ONE 11:e0152228.

Lange F, Roelofs K, Toni I (2008) Motor imagery: A window into the mechanisms and alterations of the motor system. Cortex 44:494–506.

Lehéricy S, Benali H, Moortele P-F, Pélégrini-Issac M, Waechter T, Ugurbil K, Doyon J (2005) Distinct basal ganglia territories are engaged in early and advanced motor sequence learning. P Natl Acad Sci Usa 102:12566–12571.

Li C-S, Padoa-Schioppa C, Bizzi E (2001) Neuronal Correlates of Motor Performance and Motor Learning in the Primary Motor Cortex of Monkeys Adapting to an External Force Field. Neuron 30:593–607.

Malouin F, Jackson PL, Richards CL (2013) Towards the integration of mental practice in rehabilitation programs. A critical review. Front Hum Neurosci 7:576.

Matsuzaka Y, Picard N, Strick PL (2007) Skill representation in the primary motor cortex after long-term practice. J Neurophysiol 97:1819–1832.

McInnes K, Friesen C, Boe S (2016) Specific Brain Lesions Impair Explicit Motor Imagery Ability: A Systematic Review of the Evidence. Arch Phys Med Rehabil 97:478–489.e1.

Miall RC, Wolpert DM (1996) Forward Models for Physiological Motor Control. Neural Networks 9:1265–1279.

Milton J, Solodkin A, Hluatík P, Small S (2007) The mind of expert motor performance is cool and focused. NeuroImage 35:804–813.

Mizuguchi N, Nakata H, Kanosue K (2014) Effector-independent brain activity during motor imagery of the upper and lower limbs: an fMRI study. Neurosci Lett 581:69–74.

Moran A, Guillot A, MacIntyre T, Collet C (2012) Re-imagining motor imagery: Building bridges between cognitive neuroscience and sport psychology: Re-imagining motor imagery. British Journal of Psychology 103:224–247.

Müller F, Dichgans J (1994) Dyscoordination of pinch and lift forces during grasp in patients with cerebellar lesions. Exp Brain Res 101:485–492.

Nachev P, Kennard C, Husain M (2008) Functional role of the supplementary and pre-supplementary motor areas. Nature Reviews Neuroscience 9:nrn2478.

Nakata H, Yoshie M, Miura A, Kudo K (2010) Characteristics of the athletes' brain: evidence from neurophysiology and neuroimaging. Brain Res Rev 62:197–211.

Neuper C, Wörtz M, Pfurtscheller G (2006) ERD/ERS patterns reflecting sensorimotor activation and deactivation. Progress in brain research 159:211–222.

Newell K (1991) Motor Skill Acquisition. Annual Review of Psychology 42:213–237.

Nudo, Milliken, Jenkins, Merzenich (1996) Use-dependent alterations of movement representations in primary motor cortex of adult squirrel monkeys. J Neurosci 16:785–807.

O'Shea H, Moran A (2017) Does Motor Simulation Theory Explain the Cognitive Mechanisms Underlying Motor Imagery? A Critical Review. Front Hum Neurosci 11:72.

Oostra KM, Van Bladel A, Vanhoonacker AC, Vingerhoets G (2016) Damage to Fronto-Parietal Networks Impairs Motor Imagery Ability after Stroke: A Voxel-Based Lesion Symptom Mapping Study. Front Behav Neurosci 10:5.

Padoa-Schioppa C, Li C-S, Bizzi E (2002) Neuronal Correlates of Kinematics-to-Dynamics Transformation in the Supplementary Motor Area. Neuron 36:751–765.

Padoa-Schioppa C, Li C-SRS, Bizzi E (2004) Neuronal activity in the supplementary motor area of monkeys adapting to a new dynamic environment. J Neurophysiol 91:449–473.

Pascual-Leone A, Grafman J, Hallett M (1994) Modulation of cortical motor output maps during development of implicit and explicit knowledge. Science 263:1287–1289.

Pascual-Leone A, Nguyet D, Cohen LG, Brasil-Neto JP, Cammarota A, Hallett M (1995) Modulation of muscle responses evoked by transcranial magnetic stimulation during the acquisition of new fine motor skills. J Neurophysiol 74:1037–1045.

Pfurtscheller (2001) Functional brain imaging based on ERD/ERS. Vision Res 41:1257–1260.

Pfurtscheller, da Silva FH (1999) Event-related EEG/MEG synchronization and desynchronization: basic principles. Clin Neurophysiol 110:1842–1857.

Pfurtscheller G, Neuper C (1997) Motor imagery activates primary sensorimotor area in humans. Neuroscience Letters 239:6568.

Poldrack RA, Sabb FW, Foerde K, Tom SM, Asarnow RF, Bookheimer SY, Knowlton BJ (2005) The neural correlates of motor skill automaticity. J Neurosci 25:5356–5364.

Popa LS, Ebner TJ (2018) Cerebellum, Predictions and Errors. Front Cell Neurosci 12:524.

Popa LS, Hewitt AL, Ebner TJ (2012) Predictive and feedback performance errors are signaled in the simple spike discharge of individual Purkinje cells. J Neurosci 32:15345–15358.

Popa LS, Hewitt AL, Ebner TJ (2013) Purkinje cell simple spike discharge encodes error signals consistent with a forward internal model. Cerebellum 12:331–333.

Porro C, Francescato M, Cettolo V, Diamond M, Baraldi P, Zuiani C, Bazzocchi M, Prampero P (1996) Primary motor and sensory cortex activation during motor performance and motor imagery: a functional magnetic resonance imaging study. The Journal of neuroscience 16:7688 7698.

Ptak R, Schnider A, Fellrath J (2017) The Dorsal Frontoparietal Network: A Core System for Emulated Action. Trends Cogn Sci (Regul Ed) 21:589–599.

Rizzolatti G, Matelli M (2003) Two different streams form the dorsal visual system: anatomy and functions. Experimental Brain Research 153:146–157.

Roland PE, Larsen B, Lassen NA, Skinhøj E (1980) Supplementary motor area and other cortical areas in organization of voluntary movements in man. J Neurophysiol 43:118–136.

Rosenthal CR, Kennard C, Soto D (2010) Visuospatial sequence learning without seeing. PLoS ONE 5:e11906.

Rushworth M, Krams M, Passingham R (2001) The Attentional Role of the Left Parietal Cortex: The Distinct Lateralization and Localization of Motor Attention in the Human Brain. Journal of Cognitive Neuroscience 13:698–710.

Rushworth, Nixon, Renowden, Wade, Passingham (1997) The left parietal cortex and motor attention. Neuropsychologia 35:1261–1273.

Schack T (2004) The cognitive architecture of complex movement. Int J Sport Exerc Psychology 2:403–438.

Schack T, Mechsner F (2006) Representation of motor skills in human long-term memory. Neurosci Lett 391:77–81.

Schoffelen J, Gross J (2009) Source connectivity analysis with MEG and EEG. Hum Brain Mapp 30:1857–1865.

Schuster C, Hilfiker R, Amft O, Scheidhauer A, Andrews B, Butler J, Kischka U, Ettlin T (2011) Best practice for motor imagery: a systematic literature review on motor imagery training elements in five different disciplines. BMC medicine 9:75.

Seitz RJ, Canavan AG, Yágüez L, Herzog H, Teilmann L, Knorr U, Huang Y, Hömberg V (1994) Successive roles of the cerebellum and premotor cortices in trajectorial learning. Neuroreport: An International Journal for the Rapid Communication of Research in Neuroscience.

Seitz RJ, Roland E, Bohm C, Greitz T, Stone-Elander S (1990) Motor learning in man: a positron emission tomographic study. Neuroreport 1:57–60.

Shadmehr R (2018) Motor Learning: A Cortical System for Adaptive Motor Control. Curr Biol 28:R793–R795.

Shadmehr R, Smith MA, Krakauer JW (2010) Error correction, sensory prediction, and adaptation in motor control. Annu Rev Neurosci 33:89–108.

Shmuelof L, Yang J, Caffo B, Mazzoni P, Krakauer JW (2014) The neural correlates of learned motor acuity. J Neurophysiol 112:971–980.

Sirigu A, Duhamel JR, Cohen L, Pillon B, Dubois B, Agid Y (1996) The mental representation of hand movements after parietal cortex damage. Science 273:1564–1568.

Smith AM, Dugas C, Fortier P, Kalaska J, Picard N (1993) Comparing Cerebellar and Motor Cortical Activity in Reaching and Grasping. Canadian Journal of Neurological Sciences / Journal Canadien des Sciences Neurologiques 20:S53–S61.

Smith D, Wright CJ, Cantwell C (2008) Beating the bunker: the effect of PETTLEP imagery on golf bunker shot performance. Res Q Exerc Sport 79:385–391.

Solopchuk O, Alamia A, Dricot L, Duque J, Zénon A (2017) cTBS disruption of the supplementary motor area perturbs cortical sequence representation but not behavioural performance. Neuroimage 163:34–40.

Steel A, Song S, Bageac D, Knutson KM, Keisler A, Saad ZS, Gotts SJ, Wassermann EM, Wilkinson L (2016) Shifts in connectivity during procedural learning after motor cortex stimulation: A combined transcranial magnetic stimulation/functional magnetic resonance imaging study. Cortex 74:134–148.

Tanji J, Kurata K (1982) Comparison of movement-related activity in two cortical motor areas of primates. J Neurophysiol 48:633–653.

Tanji J, Shima K (1994) Role for supplementary motor area cells in planning several movements ahead. Nature 371:413–416.

Tanji J, Shima K (1996) Supplementary motor cortex in organization of movement. Eur Neurol 36 Suppl 1:13–19.

Taylor J, Ivry R (2012) The role of strategies in motor learning. Ann Ny Acad Sci 1251:1–12.

Ungerleider LG, Doyon J, Karni A (2002) Imaging brain plasticity during motor skill learning. Neurobiol Learn Mem 78:553–564.

Wakefield C, Smith D, Moran A, Holmes P (2013) Functional equivalence or behavioural matching? A critical reflection on 15 years of research using the PETTLEP model of motor imagery. Int Rev Sport Exer P 6:105–121.

Weilke F, Spiegel S, Boecker H, von Einsiedel HG, Conrad B, Schwaiger M, Erhard P (2001) Time-resolved fMRI of activation patterns in M1 and SMA during complex voluntary movement. J Neurophysiol 85:1858–1863.

Weiss PH, Dohle C, Binkofski F, Schnitzler A, Freund HJ, Hefter H (2001) Motor impairment in patients with parietal lesions: disturbances of meaningless arm movement sequences. Neuropsychologia 39:397–405.

Wolpert DM, Miall RC, Kawato M (1998) Internal models in the cerebellum. Trends Cogn Sci (Regul Ed) 2:338–347.

Wulf G, Shea CH (2002) Principles derived from the study of simple skills do not generalize to complex skill learning. Psychonomic bulletin & review 9(2):185-211.

Wulf G, Shea C, Lewthwaite R (2010) Motor skill learning and performance: a review of influential factors: Motor skill learning and performance. Medical Education 44:75–84.

Yarrow K, Brown P, Krakauer JW (2009) Inside the brain of an elite athlete: the neural processes that support high achievement in sports. Nat Rev Neurosci 10:585–596.

Zénon A, Sidibé M, Olivier E (2015) Disrupting the Supplementary Motor Area Makes Physical Effort Appear Less Effortful. J Neurosci 35:8737–8744.

Zhang H, Xu L, Wang S, Xie B, Guo J, Long Z, Yao L (2011) Behavioral improvements and brain functional alterations by motor imagery training. Brain research 1407:38–46.

Chapter 2 : EXPERTISE MODULATES MOTOR IMAGERY-BASED BRAIN ACTIVITY

A version of this chapter has been published.
Kraeutner, S., McWhinney, S., Solomon, J., Dithurbide, L., Boe, S. (*2018*). Experience modulates motor imagery-based brain activity. *European Journal of Neuroscience.* 47(*10*), 1221-1229. doi: 10.1111/ejn.13900

2.0 ABSTRACT

Whether or not brain activation during motor imagery (MI) the mental rehearsal of movement, is modulated by experience (i.e., skilled performance, achieved through long-term practice) remains unclear. Specifically, MI is generally associated with diffuse activation patterns that closely resemble novice physical performance, which may be attributable to a lack of experience with the task being imagined vs. being a distinguishing feature of MI. We sought to examine how experience modulates brain activity driven via MI, implementing a within- and between-group design to manipulate experience across tasks as well as expertise of the participants. Two groups of 'experts' (basketball/volleyball athletes) and 'novices' (recreational controls) underwent magnetoencephalography (MEG) while performing MI of four multi-articular tasks, selected to ensure that the degree of experience that participants had with each task varied. Source-level analysis was applied to MEG data and linear mixed effects modelling was conducted to examine task-related changes in activity. Within- and between-group comparisons were completed *post-hoc* and difference maps were plotted. Brain activation patterns observed during MI of tasks for which participants had a low degree of experience was more widespread and bilateral (i.e., within-groups), with limited differences observed during MI of tasks for which participants had similar experience (i.e., between-groups). Thus, we show that brain activity during MI is modulated by experience; specifically, that novice performance is associated with the

additional recruitment of regions across both hemispheres. Future investigations of the neural correlates of MI should consider prior experience when selecting the task to be performed.

2.1 INTRODUCTION

It is well established that performance of a task for which the individual has a high degree of expertise is associated with a specific pattern of brain activity (Yarrow et al., 2009; Nakata et al., 2010; 2011). More precisely, as skilled performance is achieved through long-term practice, which we refer to throughout as ‘experience’, brain activity is more strongly lateralized and accompanied by an increased recruitment of brain regions including primary motor and somatosensory cortex, as well as the supplementary motor area, and decreased recruitment of prefrontal and cerebellar regions (Yarrow et al., 2009; Nakata et al., 2010; Dayan and Cohen, 2011). However, whether or not brain activation during motor imagery (MI), the mental rehearsal of movement absent of execution, is also modulated by experience in a manner similar to physical practice is less understood.

In general, the patterns of brain activity observed during MI more closely resemble that of novice, as opposed to experienced, physical performance, in that the brain activation patterns observed during MI are more widespread and less lateralized, including greater recruitment of bilateral parietal and frontal regions (Lacourse et al., 2005; Burianová et al., 2013; Hétu et al., 2013; Kraeutner et al., 2014). Accordingly, the diffuse and bilateral patterns of brain activation observed during MI may actually be attributable to a lack of experience with the task employed, as opposed to being a distinguishing feature of MI. Specifically, many MI tasks employed in the neuroimaging literature involve the imagined performance of a novel skill or task with which the participant has limited experience (see Hétu et al., 2013 for a review).

Indeed, neuroimaging studies comparing brain activity between novices (i.e., non-athlete controls) and experts (i.e., athletes) during MI suggest that experience is reflected in the resultant patters of brain activation. Similar to the majority of the literature applying neuroimaging to study MI (Hétu et al., 2013), resultant brain activity is shown to be more widespread for novices when comparing activation between novices and experts during MI of sport-specific skill(s) (i.e., for which the expert but not novice has a high degree of experience; Milton et al., 2007; Chang et al., 2010; Debarnot et al., 2014). However, the finding that MI of skills for which the user has a low degree of experience is associated with diffuse brain activation is confounded by limitations associated with the nature of the between-group designs. Specifically, if experience modulates MI-based brain activity, widespread brain activation should also be reflected during MI performance of experts imagining tasks in which they have a low vs. high degree of experience. Further, differences in MI-based brain activation should be abolished when experts and novices perform MI of skills for which both groups have a similar degree of experience.

Accordingly, the current study seeks to examine how experience modulates brain activity driven via MI. Here, we employed magnetoencephalography (MEG) to directly capture brain activity by assessing changes in the magnitude of ongoing cortical oscillations, known as event-related synchronization and desynchronization (ERS/ERD; Pfurtscheller and Silva, 1999; Schoffelen and Gross, 2009). It is well-established that ERD occurs over contralateral sensorimotor areas in the beta frequency band (15-30Hz) during MI, motor preparation, and execution (Pfurtscheller and Neuper, 1997; Neuper et al., 2006; Formaggio et al., 2010), and thus ERD in this frequency band is generally though to be representative of brain activation (Pfurstcheller and Neuper, 1997; Pfurtscheller and Lopes da Silva, 1999). To further elucidate the impact that experience has on MI-related brain activity, we implemented a within- and between-group design to manipulate the degree of experience that participants had with each task as well as the expertise of the participants. In particular, brain activity of ‘experts’ (varsity athletes) performing MI of a task they have a low degree of experience with was compared to that of a sport-specific task they have a high degree of experience with. To account for the sport-specific nature of the ‘expert task’, brain activity during MI was also compared between the expert task and a sport non-specific task in which the experts also have a high degree of experience with. Further, brain activity during MI was compared between experts and recreational controls (i.e., ‘non-experts’) for two tasks that all groups have similar experience with (i.e., one which all have low degree of experience with and one which all have a high degree of experience with). We hypothesized that within-group comparisons of MI-related brain activity of tasks that vary in their degree of experience will reveal widespread and bilateral patterns of brain activation, specifically encompassing activation of frontal and parietal regions (Milton et al., 2007; Chang et al., 2010; Debarnot et al., 2014). However, we further hypothesized that there would be no difference in brain activation patterns following both within- and between-group comparisons during MI of tasks that participants have similar experience with. Together, our findings will provide direct evidence that brain activation during MI is modulated by experience.

2.2 METHOD

2.2.1 Participants

Thirty right-handed (determined by the Edinburgh Handedness Inventory; Oldfield, 1971) participants who self-reported to be healthy and free of neurological disorder were recruited for the study and assigned to one of three groups. The ‘basketball’ (n=10, 8 female 20.5 ± 2.0 years) and ‘volleyball’ (n=10, 7 female 20.2 ± 1.2 years) groups were recruited from men’s and women’s basketball and volleyball teams that were part of the Atlantic University Sport (AUS) conference of U-Sports, the organization that oversees varsity sport in Canada. Participants in these athlete groups were either actively playing or had played on a varsity basketball or volleyball team within the last 2 years and continued to play recreationally. The ‘control’ group (n=10, 6 female 23.4 ± 3.4 years), recruited from the university community, were recreationally active individuals who self-identified as not having experience playing either basketball or volleyball, and thus had no experience with basketball and volleyball specific skills. Prior to the onset of the study, participants provided written, informed consent and were screened for compatibility with MEG (e.g., magnetic artefacts) according to institutional procedure. The study was conducted with approval from the Research Ethics Board at the IWK Health Centre.

2.2.2 Experimental Task

Participants underwent MEG neuroimaging while performing MI of four different tasks, selected to ensure that the degree of experience that participants had with each task varied. Tasks included two sport-specific tasks for which the two athlete groups had a high degree of experience with and the control group had a low degree of experience (free throw and overhand serve for the basketball and volleyball players, respectively), a task that all groups had a high degree of experience with (brushing your teeth), and a task that all groups had a low degree of experience (i.e., a novel task) across all groups (drawing a figure of eight in the air). The main component of each task involved MI of the dominant arm.

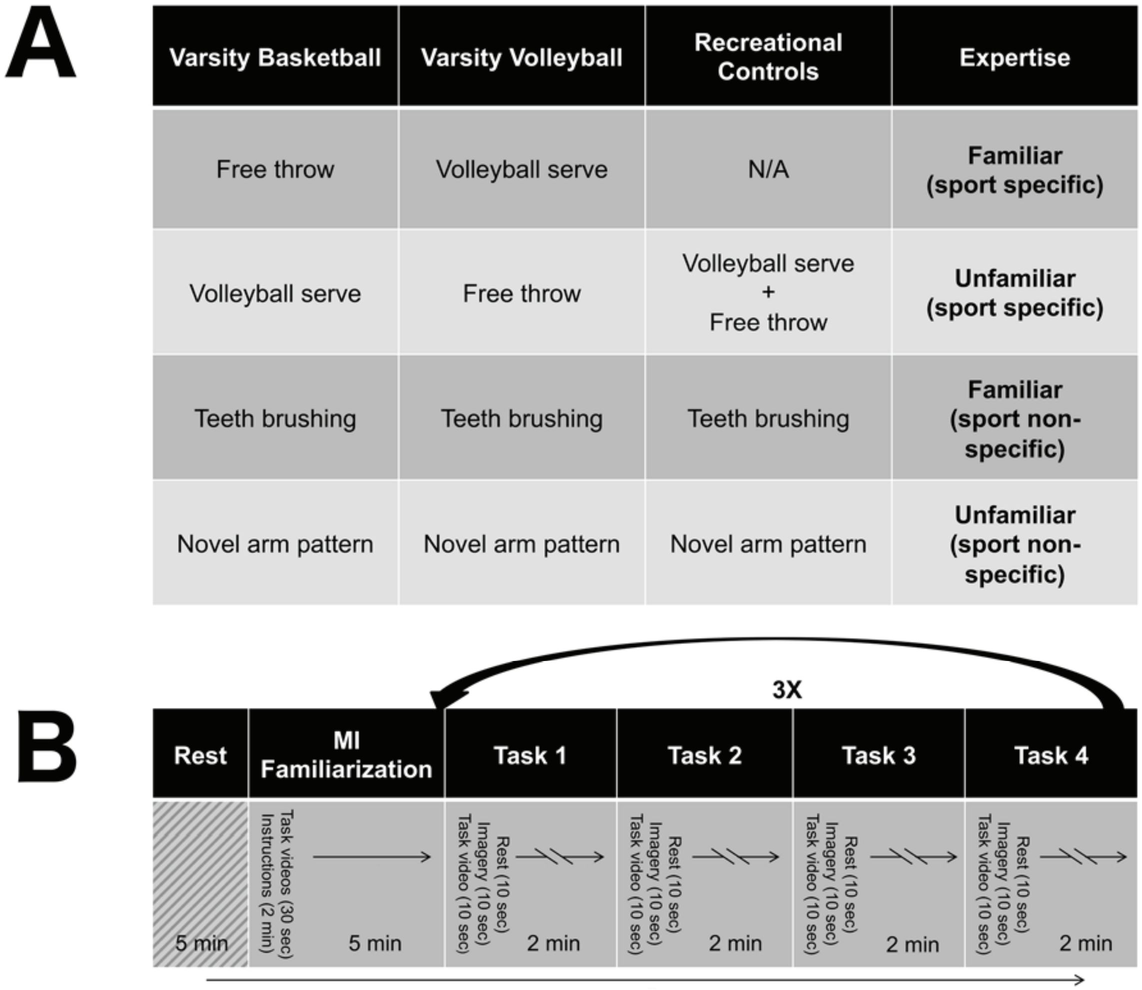
Participants performed MI of the four tasks in a block design in response to auditory cues delivered through speakers in the MEG room (Fig. 2.1). Each block consisted of six, 10s trials of MI of the same task, which alternated with a 10s rest trial for a total block duration of 120s. Each MI trial (one imagined movement) consisted of a verbalized “Go” cue, whereby participants were instructed to imagine themselves performing the corresponding movement with their eyes closed, and a “Rest” cue, whereby participants were instructed to stop imagining themselves performing the movement and to rest quietly with their eyes open. Each task block repeated three times for a total of 12 blocks (refer to Fig. 2.1). The four tasks appeared in the same order throughout the experiment for an individual participant, however, the order was randomized across participants.

2.2.3 Data Acquisition.

Neuroimaging data were collected using a 306 channel MEG system (Elekta Neuromag, FL). Electrodes placed on the skin (1 cm inter-electrode distance) overlying the right extensor carpi radialis and anterior deltoid muscles (i.e., anterior aspects of the right forearm and shoulder respectively) were used to obtain the electromyogram (EMG) in order to confirm the absence of muscle activity during MI. The vertical and horizontal electrooculogram was also obtained using electrodes placed superior and inferior to the left eye, and just lateral to the left and right eye. An electrode overlying the collarbone served as a ground. Lastly, four head position indicator (HPI) coils were affixed to the participant’s head; two on the forehead and one on each mastoid process. During scanning, HPI coils were activated continuously to generate alternating magnetic fields at frequencies between 293 and 321 Hz to track the participant’s head position. Prior to MEG scanning, three anatomical landmarks (nasion and left/right pre-auricular points), a 150-200 point head shape, and the position of the HPI coils were digitized. Event markers indicating the timing of stimuli and responses were also collected throughout. All data were acquired continuously at a sampling rate of 1500 Hz and a bandwidth of 0.1-500 Hz, and recorded to a file for offline analysis.

2.2.4 Experimental Procedure

Following informed consent and MEG screening, participants first completed the Motor Imagery Questionnaire – Revised Second Version (MIQ-RS) to assess their ability to perform MI (Gregg et al., 2005, 2010; Butler et al., 2012), and the Imagery Use Questionnaire (IUQ; Hall et al., 1990; Weinberg et al., 2003) to assess the frequency in which they employed mental practice in training. Following completion of the MIQ-RS, IUQ and MEG preparation (described above), participants were seated in the MEG and oriented to a screen placed approximately 100cm in front of the participants at eye-level that was used to visually present information. Once seated in the MEG, participants completed a MI familiarization block where participants listened to an audio recording paired with a video describing kinaesthetic MI. The recording detailed how to perform kinaesthetic MI from the first person perspective, whereby the participant is asked to picture the desired movement as though they are actually performing it (i.e., from "behind their own eyes"; Munzert and Zentgraf, 2009) while emphasizing the poly sensory aspects of the action, which has been shown to facilitate MI performance (Braun et al., 2008; Munzert and Zentgraf, 2009). Each movement (basketball free throw, volleyball serve, brushing one's teeth, and drawing a figure eight in mid-air) was then described and demonstrated in the video (from the first person perspective). Upon completion of the familiarization block, participants began the first of the twelve MI blocks.



Varsity Basketball	Varsity Volleyball	Recreational Controls	Expertise
Free throw	Volleyball serve	N/A	**Familiar (sport specific)**
Volleyball serve	Free throw	Volleyball serve + Free throw	**Unfamiliar (sport specific)**
Teeth brushing	Teeth brushing	Teeth brushing	**Familiar (sport non-specific)**
Novel arm pattern	Novel arm pattern	Novel arm pattern	**Unfamiliar (sport non-specific)**

Figure 2.1 Assigned groups and MI tasks that varied in their degree of experience across each group (A) and the timeline of the single experimental session (B). Following a familiarization period, MI was performed of the four tasks in a 12-block design.

2.2.5 Data Analysis

Analysis of the MIQ-RS scores was conducted to ensure similarity in in the ability to perform MI across groups. Scores were tabulated across participants for each imagery domain and a 2 (imagery domain) x 3 (group) mixed ANOVA was conducted to analyze the between group effects of imagery domain (kinaesthetic vs. visual) and group (basketball vs. volleyball vs. control) on MIQ-RS score. Similar to Weinberg et al., (2003), analysis of the frequency subscale of the IUQ was conducted to assess the frequency that each group used mental practice in training, to provide background information related to an individual's experience with imagery. Scores were tabulated across participants and a one-way ANOVA was conducted to analyze the between group effects of group (basketball vs. volleyball vs. control) on frequency score.

EMG signals were analyzed off-line to determine the amount of muscle activity occurring during MI performance of each task. To determine if muscle activity was present, the amplitude of the EMG signal for each channel during each trial (i.e., one imagined movement) was compared to the corresponding signal during the rest period that followed each trial. An active muscle was defined as the amplitude of EMG activity in each trial that exceeded the mean + 1 standard deviation of the activity in the rest period. Trials in which muscle activity that exceeded the threshold noted above in any EMG channel were excluded from further analysis to ensure that the resulting activation associated with each imagined movement was not 'contaminated' by overt muscle activity (Kraeutner et al., 2014). EMG activity from all trials and associated rest windows were further plotted for visual inspection to confirm the absence of EMG activity in those trials that were included. Further, any participants that showed increase in muscle activity from rest to MI in at greater than 33% of trials were excluded from further analyses (Kraeutner et al., 2014).

Head position throughout the scan was calculated and checked for each participant and block to ensure that displacement did not exceed 5mm or 3 degrees. Each participant's functional MEG data was then co-registered to a template brain (TT_avg152T1) based on the digitized anatomical landmarks and head shape, using software supplied by the MEG vendor (MRIlab, Elekta Neuromag, FL). MEG data were low-pass filtered (70 Hz) and down-sampled to 250 Hz, and a 15-30Hz band-pass filter applied. For the purposes of this analysis, MI and rest intervals were defined to be seven seconds of data: the onset was defined as 2 seconds after the 'Go' or 'Rest' cue respectively, to 1 second preceding the next cue. These intervals were chosen to avoid transient brain responses at trial onset, and anticipatory responses prior to the cue.

As previously stated, oscillatory activity in the beta frequency band is inhibitory, thus ERD in this frequency band is generally thought to be representative of brain activation (Pfurtscheller and Neuper, 1997; Pfurtscheller and Lopes da Silva, 1999). Changes in beta power observed in the present study are referred to throughout as brain activity. To assess changes in brain activity, whole head dual-state beamformer was applied (Vrba et al., 2010; Diwakar et al. 2011a,b). The beamformer approach involves the reconstruction of the contribution of a single location to the measured field at a given moment in time, generating pseudo-*Z* values that represent estimated neuronal activity at the specified source. Thus, resultant source-level maps representing the change in magnitude of the beta rhythm (i.e., ERS/ERD) during MI as compared to the respective rest interval were generated for each participant and task, and pseudo-*Z* values generated from the beamformer were used for the purposes of group analyses (see Fig. 2.2 for an overview of the analysis pipeline). Prior to the source-level analysis, we generated time-frequency response plots (also in the beta frequency band, averaged across 50 MEG sensors centred on the midline and encompassing bilateral sensorimotor areas) at the sensor-level for each task and group. These plots are included as Supplementary Materials (Appendix A; Fig. 6.1).

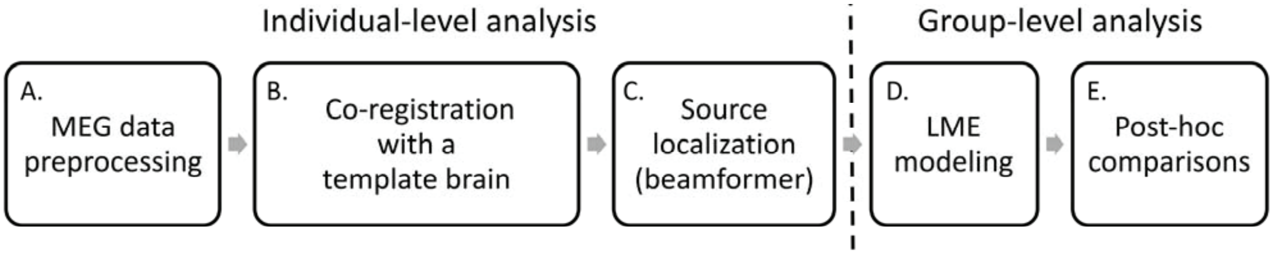


Figure 2.2 Overview of the analysis pipeline. Following data preprocessing (A) and co-registration of the MEG data with a template brain for each individual dataset (B), whole head dual-state beamformer was applied to MI and rest intervals to generate individual source-level activation maps and resulting pseudo-z values for each task (C). The pseudo-z values from the individual source-level activation maps were input to each model (i.e., at each voxel) (D), and post-hoc test were completed within each model using t-tests of the model estimates.

Task-related changes in beamformer pseudo-*Z* values were evaluated using linear mixed effects modeling, with the *lme4* package (Bates et al., 2015) in R version 3.2.4 (R Development Core Team, 2013). A base model assessed pseudo-*Z* as a function of group, task, their interaction, and a random intercept for each participant. In addition, models were created with terms for participant sex, age, a fixed effect of block number, or a random block-by-subject slope. The fit of each model was measured using the Akaike Information Criterion (Akaike, 1974), which evaluates a model's log-likelihood against penalties for added terms, in order to select the most descriptive and parsimonious model. The base model was not significantly improved by any of the alternatives, and so age, sex and block number were not included in further models.

A separate model was created for each voxel in order to investigate the spatial distribution of effects. Activity maps related to between-group and -task contrasts were generated by plotting the significance (*p*) of task- or group-related effects on a per-voxel basis. Within- and between-group comparisons were completed *post-hoc*. All per-voxel comparisons were investigated as one-tailed *t*-tests on model estimates, and familywise error was controlled in each model using the Holm-Bonferroni method, at a corrected significance threshold of $p < .05$ (Holm, 1979). Task-related effects were plotted as 1 – corrected p for each comparison, and the significance of voxel clusters was determined using 3DClustSim (Forman et al., 1995) in AFNI (Cox, 1996) at a corrected cluster significance threshold of $p < .05$. Significant voxel clusters were then assigned to a brain region by overlaying the Harvard-Oxford Cortical Structural atlas (Frazier et al., 2005; Desikan et al., 2006; Makris et al., 2006; Goldstein et al., 2007; first transformed to Talairach space) on these difference maps. Importantly, regions were only included if they exceeded the threshold for a significant cluster.

2.3 RESULTS

2.3.1 Imagery Ability and Frequency of Use

All groups were similarly able to perform MI evidenced by MIQ-RS scores in both the visual and kinaesthetic domains (see Table 2.1). No main effects were found for imagery domain [F(1, 29) = 1.08, $p = 0.31$] nor group [F(2, 29) = 0.14, $p = 0.87$], and the interaction between imagery domain and group was not significant [F(2, 29) = 0.77, $p = 0.47$]. As the IUQ data were not normally distributed, we used the Wilcoxon rank sum test to compare the frequency scores between each group (Table 2.1). While no differences were observed between the basketball and volleyball groups ($Z = -0.53$, $p = 0.60$), or between the basketball and control groups ($Z = -1.82$, $p = 0.69$), a significant difference was observed between the volleyball and control groups ($Z = -2.31$, $p = 0.02$).

No participants were excluded from the analysis for demonstrating overt muscle activity as per our criteria (i.e., activity in >33% of MI trials). For the basketball group a total of 11 trials were rejected, corresponding to 1.5% of the total number of trials performed (720). For the volleyball group, a total of 17 trials were rejected, corresponding to 2.4% of the total trials. For the control group, 11 trials were rejected, corresponding to 1.5% of the total number of trials.

Table 2.1

MIQ-RS and IUQ Frequency Scores for each group.

Group	Mean Visual MI Score /49 (SD)	Mean Kinaesthetic MI Score /49 (SD)	Mean IUQ Frequency Score /84 (SD)
Control	39 (6.7)	37.8 (10.5)	30.9 (19.3)
Volleyball	37.4 (8.0)	38.1 (5.5)	54.6 (11.4)
Basketball	38.5 (4.7)	35.3 (4.8)	48.8 (7.7)

2.3.2 Group-level MEG results

Table 2.2 summarizes the within- and between-group comparisons, and Figures 2.3 and 2.4 depict the task-related effects plotted as 1 – corrected *p* for each comparison. Within-group comparisons revealed activation in a number of additional regions, including ipsilateral frontal and parietal regions, for the task that participants had a low vs. high degree of experience thus indicating a more widespread and bilateral pattern of activation during novice performance (Fig. 2.3). Interestingly, no differences were observed within the expert groups for the sport specific vs. non-specific expert tasks (see Table 2.2).

Between-group comparisons during MI of the two tasks that all groups had equal experience with (e.g., "teeth brushing" and "novel arm pattern") revealed limited differences. Specifically, differences were only detected when comparing basketball and control groups, localized to the ipsilateral hemisphere (Fig. 2.4). Importantly, comparisons were also conducted between the two expert groups during MI of the sport-specific skills (e.g., "free throw" and "serve"), to control for sport-specific expertise. Interestingly, during MI of the basketball-specific skill, significant differences were observed in that greater recruitment of five ipsilateral regions resulted for the volleyball group. However, no differences between expert groups were observed during MI of the volleyball-specific skill. Tables 2.3 and 2.4 summarize the number of significant voxels by region and hemisphere for comparisons that demonstrated at least one significantly different cluster of activation (Forman et al., 1995).

Table 2.2

Summary of within- and between-group comparisons. Three within-group comparisons (i.e., across task) and three between-group comparisons resulted in significant differences in brain activation.

Within-Group Comparisons	
Differences	No differences
Basketball: Novel task > Free throw	Basketball: Teeth brushing > Free throw
Volleyball: Novel task > Overhand serve	Volleyball: Teeth brushing > Overhand serve
Control: Novel task > Teeth brushing	
Between-Group Comparisons	
Differences	No differences
Novel task: Control > Basketball	Teeth task: Control > Volleyball
Teeth brushing: Control > Basketball	Novel task: Control > Volleyball
Free throw: Volleyball > Basketball	Overhand serve: Basketball > Volleyball

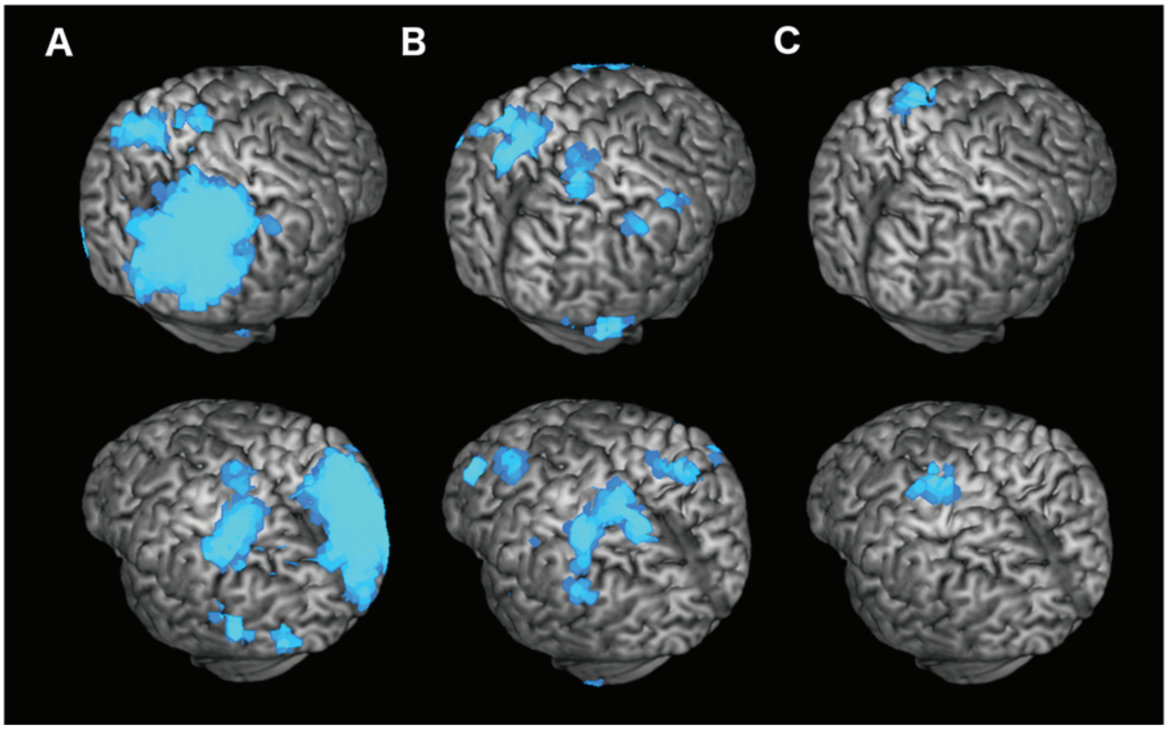


Figure 2.3 Differences in activation shown between the task with low vs. high degree of experience (plotted as 1 – corrected p) within the A) basketball, B) volleyball, and C) control group. Regions additionally recruited during the novel task include bilateral posterior parietal regions and the right SMA for the basketball group (A; free throw vs. novel), bilateral poster parietal regions for the volleyball group (B; serve vs. novel), and activation localized to the left precentral gyrus for the control group (C; teeth brushing vs. novel).

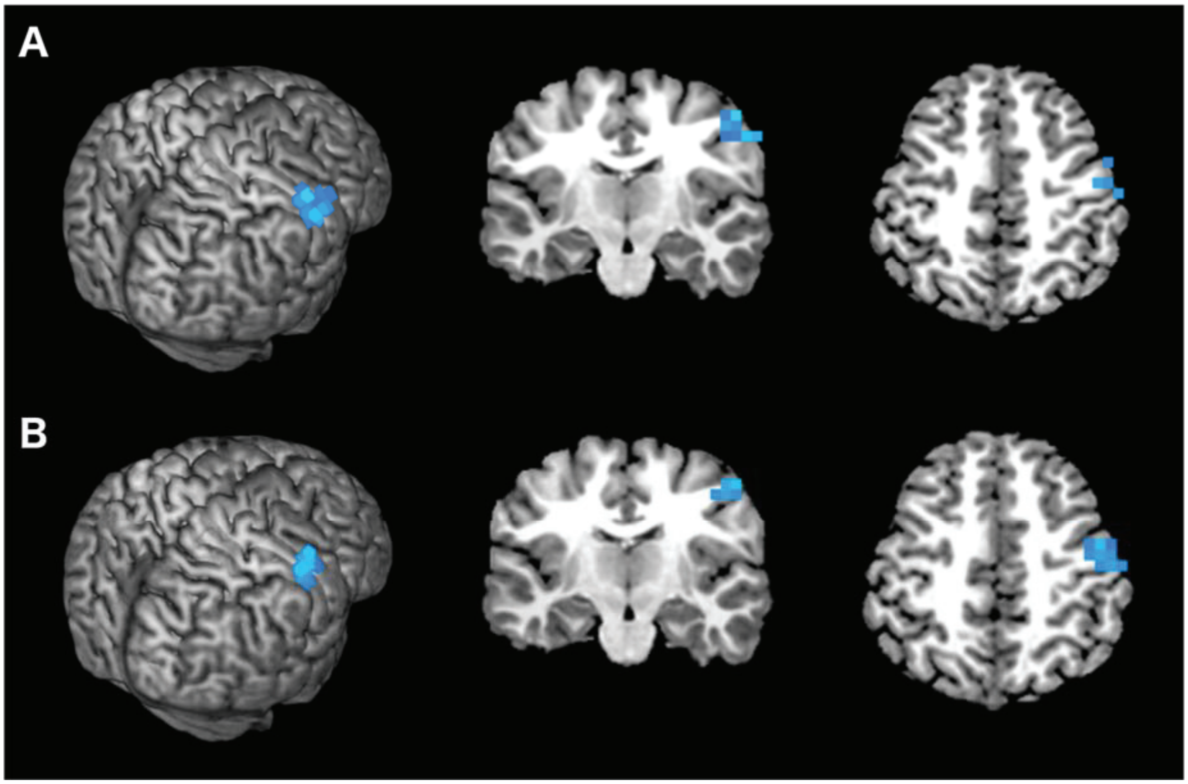


Figure 2.4 Differences in activation (plotted as 1 – corrected p) shown between the basketball and control groups, whereby additional activation localized to the ipsilateral precentral and postcentral gyri was observed in the control group during both A) the task unfamiliar to all groups (novel) and B) the task that all groups had a high degree of experience with (teeth brushing).

Table 2.3

Within-group comparisons that resulted in at least one significantly different cluster of activation. The number of voxels with differences in activation is displayed as a function of brain region and hemisphere.

	Number of significant voxels					
	Basketball group: Novel > Free throw		Volleyball group: Novel > Serve		Control group: Novel > Teeth	
Region	Contralateral (L)	Ipsilateral (R)	Contralateral (L)	Ipsilateral (R)	Contralateral (L)	Ipsilateral (R)
Frontal Pole	-	-	24	-	-	-
Insular Cortex	-	-	15	-	-	-
Superior Frontal Gyrus	-	-	24	-	-	-
Middle Frontal Gyrus	-	-	24	-	-	-
Inferior Frontal Gyrus, pars opercularis	-	-	-	6	-	-
Middle Temporal Gyrus (temporooccipital)	9	-	-	6	-	-
Inferior Temporal Gyrus (temporooccipital)	6	-	-	22	-	-
Precentral Gyrus	39	-	15	16	18	-
Postcentral Gyrus	38	-	50	29	-	-
Supplementary Motor Cortex	-	10	-	-	-	-

Superior Parietal Lobule	78	53	52	12	-	-
Supramarginal Gyrus (anterior)	18	7	-	-	-	-
Supramarginal Gyrus (posterior)	27	22	-	6	-	-
Angular Gyrus	38	54	18	-	-	-
Heschl's Gyrus	-	-	-	-	-	-
Lateral Occipital Cortex (superior)	22	292	17	7	-	-
Lateral Occipital Cortex (inferior)	44	10	-	10	-	-
Intracalcarine Cortex	-	24	-	15	-	-
Paracingulate Gyrus	-	-	16	10	-	-
Cingulate Gyrus (anterior)	27	33	45	68	-	-
Cingulate Gyrus (posterior)	6	27	16	39	-	-
Precuneus Cortex	6	112	9	29	-	-
Cuneal Cortex	-	37	-	-	-	-
Lingual Gyrus	7	9	-	49	-	-
Temporal Occipital Fusiform Cortex	15	13	-	26	-	-
Occipital Fusiform Gyrus	15	-	-	20	-	-
Parietal Operculum Cortex	6	-	-	-	-	-
Occipital Pole	-	61	-	-	-	-

Table 2.4

Between-group comparisons that resulted in at least one significantly different cluster of activation. The number of voxels with differences in activation is displayed as a function of brain region by hemisphere.

	Number of significant voxels					
	Novel task: Control > Basketball		Teeth brushing: Control > Basketball		Free throw: Volleyball > Basketball	
Region	Contralateral (L)	Ipsilateral (R)	Contralateral (L)	Ipsilateral (R)	Contralateral (L)	Ipsilateral (R)
Insular Cortex	-	-	-	-	-	10
Precentral Gyrus	-	10	-	7	-	18
Postcentral Gyrus	-	8	-	6	-	9
Supramarginal Gyrus (posterior)	-	-	-	-	-	10
Angular Gyrus	-	-	-	-	-	9

2.4 DISCUSSION

The current study implemented a within- and between-group design to examine the extent to which experience (i.e., skilled performance, gained through long-term practice) modulates MI-related brain activity as assessed via changes in beta power. To achieve this objective, we manipulated the degree to which each participant had experience with each task (i.e., within-groups) while controlling for expertise amongst participants (i.e., between-groups). Importantly, employing a within-group design allowed us to examine experience in the context of task in addition to group-level expertise, thus, addressing limitations of previous studies investigating MI-related brain activation between experts and novices that used only a between-group design. As hypothesized, the brain activation pattern observed during MI of a task for which participants had a low degree of experience was more widespread and bilateral in nature relative to the pattern observed during MI of a task for which they had a high degree of experience (i.e., the within-group comparison; Table 2.3). Coupled with the lack of differences during MI of tasks to which participants had similar experience (both within- and between-groups), we provide direct evidence that brain activation patterns observed during MI are modulated by experience.

2.4.1 Experience-related brain activity

Consistent with previous between-group findings showing increased overall brain activation between novice and experts performing MI of 'expert skills' (Milton et al., 2007; Chang et al., 2010; Debarnot et al., 2014), we show that additional brain regions are recruited when experts perform MI of a novel task in comparison to when they perform MI of the skill for which they have expertise. Specifically, difference maps comparing MI of tasks with a low vs. high degree of experience within the expert groups revealed additional recruitment of bilateral parietal, bilateral cingulate, ipsilateral posterior parietal and lateral occipital regions, as well as core motor regions (i.e., clusters localized to contralateral precentral and postcentral gyri; see Fig. 2.3). Additionally, differences localized to contralateral frontal regions in the volleyball group and temporal regions in the basketball group were also observed. Importantly, no differences were observed when comparing brain activation between tasks for which the experts had a similar degree of experience (i.e., their sport specific and sport non-specific task; see Table 2.2). Critically, this finding allows us to conclude that it is experience with the task and not the sport-specific nature of the 'expert' task that modulates brain activity driven via MI. The recruitment of additional regions across both hemispheres that we observed between tasks with a low vs. high degree of experience are in alignment with previous literature that suggests brain activation during novice performance reflects an inefficient and unorganized network (Haufler et al., 2000; Milton et al., 2007; Percio et al., 2008; Del Percio et al., 2010; Bar and DeSouza, 2016; Guo et al., 2017), and that greater recruitment of bilateral regions involved in motor planning may be indicative of the additional 'effort' required (Milton et al., 2007; Percio et al., 2008; Del Percio et al., 2010; Guo et al., 2017).

While we attempted to use tasks that had similar characteristics (i.e., all tasks were multi-articular and primarily involved performance with the dominant arm), the between-group comparisons allowed us to ensure that differences in brain activation were indeed modulated by experience as opposed to the task being imagined. As detailed in Table 2.4, between-group comparisons revealed limited differences when comparing brain activation across tasks that all groups had a similar level of experience with, namely two clusters of activation localized over the ipsilateral pre- and post- central gyri that were observed in the novice group. While the comparison of activation patterns between the volleyball and control groups may have been influenced by the differing levels of experience with MI (as frequency scores from the IUQ were shown to be different), no difference in activation patterns were noted between these groups (see Table 2.2 and Table 2.4). While the observation of these two clusters of activation indicate additional recruitment of ipsilateral motor and sensory regions for the novice but not expert groups, the finding is likely attributable to the focus point of the imagined performance. Namely, as greater recruitment of ipsilateral post central gyrus has been demonstrated between transitive (i.e., involving an object) vs. intransitive MI, these differences may be driven by a greater focus on the object in the novice group only. Yet, while we can only speculate as to how different focus points may further modulate MI-related brain activity, future research should examine the impact of shifting the focus point of the MI performance on brain activation driven via MI.

2.4.2 Task Importance in MI Literature

Relative to physical practice, the pattern of brain activity generally observed during MI is more bilateral and widespread, which more closely resembles novice physical performance (Lacourse et al., 2005; Burianová et al., 2013; Hétu et al., 2013; Kraeutner et al., 2014). In light of the current findings however, it is suggested that the generally widespread patterns of brain activity observed during MI could be attributed to a lack of experience with the task being imagined. Specifically, previous research has demonstrated changes in brain activation observed during MI following physical practice of the skill being imagined (Lafleur et al., 2002; Lacourse et al., 2005). After engaging in five sessions of physical practice on a key-press sequence task, Lacourse et al. (2005) demonstrated that decreases in activation of bilateral frontal and parietal regions were observed during MI. Lafleur et al. (2002) also demonstrate experience-related changes in brain activation during MI following a single session of physical practice on a foot sequence task. Coupled with an increase in activity localized to medial orbitofrontal and striatal regions, decreased activity was demonstrated within the (ipsilateral) left inferior parietal lobule and cerebellum.

Studies using MI as a model to track changes in brain activation throughout physical training further support that brain activity driven via MI is modulated by experience. Specifically, by assessing brain activation (localized to the SMA and auditory regions) during MI at multiple time points while professional ballet dancers physically trained on a new dance (Bar and DeSouza, 2016), it was shown that a global decrease within the network of SMA and auditory regions occurs when comparing MI-related brain activation from pre- to post-training. Interestingly, an overall *increase* within this network was initially observed during MI during the early stages of training, a pattern similarly shown in Baeck et al. (2012) when comparing brain activation during MI before and after novices trained on a shooting task. Thus, while there is undoubtedly brain activation specific to processes that underlie MI (Hétu et al., 2013; Kraeutner et al., 2016; Oostra et al., 2016; Ptak et al., 2017), the diffuse patterns of activity generally observed during MI may not be purely indicative of a difference between MI and physical practice. Instead, we suggest that these patterns are also influenced by the degree to which the user is experienced with the skill.

Expanding our understanding of how experience with the task being imagined affects MI-related brain activity has implications for the way MI is used in different disciplines. For instance, when MI is used in post-stroke rehabilitation, the tasks being imagined are not often tailored to participants prior experience or interests (which often aligns with prior experience; (Page et al., 2007, 2011; Riccio et al., 2010; Ietswaart et al., 2011) despite this being a core principle of task specific physical therapies (Page et al., 2013). Given the present results, using tasks in which participants have prior experience may focus brain activity to regions critical for task performance, which in the context of rehabilitation can aid in driving plasticity necessary for functional recovery to occur. Future research could include evaluation of the clinical efficacy of MI-based therapies that employ tasks in which the participant has prior experience, as this approach may well improve on the somewhat mixed results seen for MI in functional recovery post-stroke.

2.4.3 Limitations

It is important to take into consideration the advantage that athletes may have over non-athlete (control) participants in performing imagery, as no imagery training itself was employed in the present work. However, we provided participants with a familiarization period in which they were instructed on how to perform MI, and any potential confounds were further mitigated as imagery ability was shown to be equivalent across groups (see Table 2.3; Gregg et al., 2005, 2010). In addition, it is likely that the sport non-specific task that all participants had a high degree of experience (i.e., teeth brushing) was less complex than the other tasks employed. While we employed tasks with a similar degree of kinematic complexity, it is possible that differences in complexity may contribute in part to one of our findings, namely limited differences in brain activation patterns noted across tasks within the control group (i.e., sport non-specific vs. novel). For instance, Gibson et al. (2014) assessed task-driven differences in ERS/ERD at the sensor level during MI, and showed that imagery of a complex task produced greater and more sustained ERS/ERD in comparison to imagery of a simple task. However, we can reasonably conclude that the limited differences observed in the control group are not modulated by complexity, as we showed no differences in brain activation within the expert groups when comparing the sport non-specific skill (teeth brushing) to its sport-specific counterpart, which could be considered a more complex skill to perform. Nonetheless, assessing MI-related brain activation as a function of task complexity is an important avenue of future research.

2.4.4 Conclusion

The current study informs on the neural correlates associated with MI. Specifically, during MI, novice performance is associated with widespread and bilateral activity, primarily in frontal and parietal regions. Taken together with previous literature demonstrating changes in MI-related brain activation throughout physical training, we conclude that brain activity driven via MI is modulated by experience. Further, as many MI tasks employed in the neuroimaging literature involve novel skills with which the participant has limited experience with, we conclude that the resulting patterns reflect of a novice level of performance in addition to pure differences between MI and physical practice. Thus, future work investigating MI-related brain activation should consider prior experience when selecting the MI task to be performed.

2.5 REFERENCES

Akaike, H (1974). A new look at the statistical model identification. IEEE Trans. Automat Contr 19:716–723.

Baeck, J-SS, Kim, Y-TT, Seo, J-HH, Ryeom, H-KK, Lee, J, Choi, S-MM, Woo, M, Kim, W, Kim, JG, Chang, Y (2012) Brain activation patterns of motor imagery reflect plastic changes associated with intensive shooting training. Behav Brain Res 234:26–32.

Bar RJ, DeSouza JF (2016) Tracking Plasticity: Effects of Long-Term Rehearsal in Expert Dancers Encoding Music to Movement. PLoS ONE 11:e0147731.

Bates, D, Maechler, M, Bolker, B (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67(1):1-48.

Braun S, Kleynen M, Schols J, Schack T, Beurskens A, Wade D (2008) Using mental practice in stroke rehabilitation: a framework. Clin Rehabil 22:579–591.

Burianová H, Marstaller L, Sowman P, Tesan G, Rich A, Williams M, Savage G, Johnson B (2013) Multimodal functional imaging of motor imagery using a novel paradigm. NeuroImage 71:50–58.

Butler A, Cazeaux J, Fidler A, Jansen J, Lefkove N, Gregg M, Hall C, Easley K, Shenvi N, Wolf S (2012) The Movement Imagery Questionnaire-Revised, Second Edition (MIQ-RS) Is a Reliable and Valid Tool for Evaluating Motor Imagery in Stroke Populations. Evid-based Compl Alt 2012:1–11.

Chang Y, Lee J-J, Seo J-H, Song H-J, Kim Y-T, Lee H, Kim H, Lee J, Kim W, Woo M, Kim J (2010) Neural correlates of motor imagery for elite archers. NMR in Biomedicine 24:366-72.

Dayan E, Cohen LG (2011) Neuroplasticity subserving motor skill learning. Neuron 72:443–454.

Debarnot U, Sperduti M, Di Rienzo F, Guillot A (2014) Experts bodies, experts minds: How physical and mental training shape the brain. Front Hum Neurosci 8:280.

Del Percio C, Infarinato F, Iacoboni M, Marzano N, Soricelli A, Aschieri P, Eusebi F, Babiloni C (2010) Movement-related desynchronization of alpha rhythms is lower in athletes than non-athletes: a high-resolution EEG study. Clin Neurophysiol 121:482–491.

Desikan RS, Ségonne F, Fischl B, Quinn BT, Dickerson BC, Blacker D, Buckner RL, Dale AM, Maguire RP, Hyman BT, Albert MS, Killiany RJ (2006) "An automated labeling system for subdividing the human cerebral cortex on MRI scans into gyral based regions of interest." Neuroimage 31(3):968-980.

Diwakar, M, Huang, M-X, Srinivasan, R, Harrington, DL, Robb, A, Angeles, A, Muzzatti, L, Pakdaman, R, Song, T, Theilmann, RJ, Lee, RR (2011a) Dual-Core Beamformer for obtaining highly correlated neuronal networks in MEG. Neuroimage 54:253–263.

Diwakar, M, Tal, O, Liu, TT, Harrington, DL, Srinivasan, R, Muzzatti, L, Song, T, Theilmann, RJ, Lee, RR, Huang, MX (2011b) Accurate reconstruction of temporal correlation for neuronal sources using the enhanced dual-core MEG beamformer. Neuroimage 56:1918–1928.

Formaggio, E, Storti, SF, Cerini, R, Fiaschi, A, Manganotti, P (2010) Brain oscillatory activity during motor imagery in EEG-fMRI coregistration. Magnetic Resonance Imaging 28(10):1403–12.

Forman, SD, Cohen, JD, Fitzgerald, M, Eddy, WF, Mintun, MA, Noll, DC (1995) Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): use of a cluster-size threshold. Magn Reson Med 33:636-647.

Frazier JA, Chiu S, Breeze JL, Makris N, Lange N, Kennedy DN, Herbert MR, Bent EK, Koneru VK, Dieterich ME, Hodge SM, Rauch SL, Grant PE, Cohen BM, Seidman LJ, Caviness VS, Biederman J (2005) Structural brain magnetic resonance imaging of limbic and thalamic volumes in pediatric bipolar disorder. Am J Psychiatry 162(7):1256-1265.

Gibson, RM, Chennu, S, Owen, AM, Cruse, D (2014) Complexity and familiarity enhance single-trial detectability of imagined movements with electroencephalography. Clin Neurophysiol 125:1556–1567.

Goldstein JM, Seidman LJ, Makris N, Ahern T, O'Brien LM, Caviness VS Jr, Kennedy DN, Faraone SV, Tsuang MT (2007) Hypothalamic abnormalities in schizophrenia: sex effects and genetic vulnerability. Biol Psychiatry 61(8), 935-945.

Gregg M, Hall C, Butler A (2010) The MIQ-RS: A Suitable Option for Examining Movement Imagery Ability. Evid Based Complement Alternat Med 7:249–257.

Gregg M, Hall C, Nederhof E (2005) The imagery ability, imagery use, and performance relationship. The Sport Psychologist 19:93–99.

Guo Z, Li A, Yu L (2017) “Neural Efficiency” of Athletes’ Brain during Visuo-Spatial Task: An fMRI Study on Table Tennis Players. Front Behav Neurosci 11:72.

Haufler AJ, Spalding TW, Santa Maria DL, Hatfield BD (2000) Neuro-cognitive activity during a self-paced visuospatial task: comparative EEG profiles in marksmen and novice shooters. Biol Psychol 53:131–160.

Hall C, Rodgers W, Barr K (1990) The use of imagery by athletes in selected sports. The Sport Psychologist 4:1–10.

Hétu S, Grégoire M, Saimpont A, Coll M-P, Eugène F, Michon P-E, Jackson P (2013) The neural network of motor imagery: An ALE meta-analysis. Neuroscience and biobehavioral reviews 37:930–949.

Ietswaart M, Johnston M, Dijkerman HC, Joice S, Scott CL, MacWalter RS, Hamilton SJ (2011) Mental practice with motor imagery in stroke recovery: randomized controlled trial of efficacy. Brain 134:1373–1386.

Kraeutner S, Gionfriddo A, Bardouille T, Boe S (2014) Motor imagery-based brain activity parallels that of motor execution: Evidence from magnetic source imaging of cortical oscillations. Brain research 1588:81–91.

Kraeutner SN, Keeler LT, Boe SG (2016) Motor imagery-based skill acquisition disrupted following rTMS of the inferior parietal lobule. Experimental brain research 234:397–407.

Lacourse MG, Orr EL, Cramer SC, Cohen MJ (2005) Brain activation during execution and motor imagery of novel and skilled sequential hand movements. Neuroimage 27:505–519.

Lafleur MF, Jackson PL, Malouin F, Richards CL, Evans AC, Doyon J (2002) Motor learning produces parallel dynamic functional changes during the execution and imagination of sequential foot movements. Neuroimage 16:142–157.

Makris N, Goldstein JM, Kennedy D, Hodge SM, Caviness VS, Faraone SV, Tsuang MT, Seidman LJ (2006) "Decreased volume of left and total anterior insular lobule in schizophrenia." Schizophr Res 83(2-3):155-171.

Milton J, Solodkin A, Hluatík P, Small S (2007) The mind of expert motor performance is cool and focused. NeuroImage 35:804–813.

Munzert J, Zentgraf K (2009) Motor imagery and its implications for understanding the motor system. Progress in Brain Research 174:219–229.

Nakata H, Yoshie M, Miura A, Kudo K (2010) Characteristics of the athletes' brain: evidence from neurophysiology and neuroimaging. Brain Res Rev 62:197–211.

Neuper, C, Wörtz, M, Pfurtscheller, G (2006) ERD/ERS patterns reflecting sensorimotor activation and deactivation. Progress in Brain Research 159:211–22.

Oldfield RC (1971) The assessment and analysis of handedness: The Edinburgh inventory. Neuropsychologia 9:97113.

Oostra KM, Van Bladel A, Vanhoonacker AC, Vingerhoets G (2016) Damage to Fronto-Parietal Networks Impairs Motor Imagery Ability after Stroke: A Voxel-Based Lesion Symptom Mapping Study. Front Behav Neurosci 10:5.

Page SJ, Boe S, Levine P (2013) What are the "ingredients" of modified constraint-induced therapy? An evidence-based review, recipe, and recommendations. Restor Neurol Neurosci 31:299–309.

Page SJ, Dunning K, Hermann V, Leonard A, Levine P (2011) Longer versus shorter mental practice sessions for affected upper extremity movement after stroke: a randomized controlled trial. Clin Rehabil 25:627–637.

Page SJ, Levine P, Leonard A (2007) Mental practice in chronic stroke: results of a randomized, placebo-controlled trial. Stroke 38:1293–1297.

Percio C, Rossini P, Marzano N, Iacoboni M, Infarinato F, Aschieri P, Lino A, Fiore A, Toran G, Babiloni C, Eusebi F (2008) Is there a "neural efficiency" in athletes? A high-resolution EEG study. Neuroimage 42:1544–1553.

Pfurtscheller, G, Lopes da Silva, FH (1999) Event-related EEG/MEG synchronization and desynchronization: basic principles. Clinical Neurophysiology : Official Journal of the International Federation of Clinical Neurophysiology 110(11):1842–57.

Pfurtscheller, G, Neuper, C (1997) Motor imagery activates primary sensorimotor area in humans. Neuroscience Letters 239(2-3):65–8.

Ptak R, Schnider A, Fellrath J (2017) The Dorsal Frontoparietal Network: A Core System for Emulated Action. Trends Cogn Sci (Regul Ed) 21:589–599.

Riccio I, Iolascon G, Barillari MR, Gimigliano R, Gimigliano F (2010) Mental practice is effective in upper limb recovery after stroke: a randomized single-blind cross-over study. Eur J Phys Rehabil Med 46:19–25.

Schoffelen, JM, Gross, J (2009) Source connectivity analysis with MEG and EEG. Human Brain Mapping 30(6):1857–65.

Vrba J, Taulu S, Nenonen J, Ahonen A (2010) Signal space separation beamformer. Brain Topogr 23:128–133.

Weinberg, R, Butt, J, Knight, B, Burke, K, Jackson, A (2003) The relationship between the use and effectiveness of imagery: an exploratory investigation. Journal of Applied Sport Psychology 15:26–40.

Yarrow K, Brown P, Krakauer JW (2009) Inside the brain of an elite athlete: the neural processes that support high achievement in sports. Nat Rev Neurosci 10:585–596.

Chapter 3 : NEURAL AND BEHAVIOURAL OUTCOMES DIFFER FOLLOWING EQUIVALENT BOUTS OF MOTOR IMAGERY OR PHYSICAL PRACTICE

3.0 ABSTRACT

Despite its reported effectiveness for the acquisition of motor skills, we know little about how MI-based brain activation and performance evolves when motor imagery (MI, the imagined performance of a motor task) is used to learn a complex motor skill compared to physical practice (PP). The current study examined changes in MI-related brain activity and performance driven by an equivalent bout of MI or PP-based training. Participants (*N* = 24) engaged in five days of either MI or PP of a dart throwing task. Brain activity (via functional magnetic resonance imaging; fMRI) and performance-related outcomes were obtained pre/post training. Relative to PP, MI-based training did not drive robust changes in brain activation and was inferior for realizing improvements in performance: greater activation in regions critical to refining the motor program were observed in the PP vs. MI group post-training, and MI led to smaller improvements in performance relative to PP. Findings indicate that the modality of practice (i.e., MI vs. PP) used to learn a complex motor skill manifests as differences in both resultant patterns of brain activity and performance. Ultimately, by directly comparing brain activity and behavioural outcomes after equivalent training through MI vs. PP, this work provides unique knowledge regarding the neural mechanisms underlying learning through MI.

3.1 INTRODUCTION

Substantial evidence indicates reliable changes of brain activation result from motor skill learning (Ungerleider et al., 2002; Doyon and Benali, 2005; Dayan and Cohen, 2011). With repeated practice, novices move along the expertise continuum, realizing improvements in performance coincident with brain activity that is decreased in magnitude, particularly in cortical areas, and more strongly lateralized (contralateral) to the effector used in the task (Yarrow et al., 2009; et al., 2010; Dayan and Cohen, 2011). While our knowledge of how performance and brain activation patterns evolve as learning occurs is derived almost exclusively from studies employing physical practice (PP), the 'gold standard' to learn a motor skill, motor imagery (MI; the imagined performance of a motor task) is often used during assessments of brain activation as many complex motor skills cannot be performed in the various neuroimaging environments (e.gs., functional magnetic resonance imaging (fMRI), magnetoencephalography; see(Wei and Luo, 2010; Baeck et al., 2012) for examples). However, one unknown factor related to motor skill learning is how the modality in which the individual practices (MI vs. PP) modulates changes in both performance and MI-based brain activity. Specifically, despite evidence showing the effectiveness of MI in motor skill learning (Driskell et al., 1994; Schuster et al., 2011; Di Rienzo et al., 2016; Ruffino et al., 2017), we know comparatively little about the evolution of performance and MI-based brain activation patterns when this modality of practice is used to facilitate learning of a complex motor skill (Frank and Schack, 2017; Ruffino et al., 2017)

Indeed, recent work indicates that expertise modulates patterns of MI-based brain activation (Milton et al., 2007; Chang et al., 2010; Debarnot et al., 2014; Kraeutner et al., 2018). In particular, when varsity athletes performed MI of their sport-specific skills compared to a novel task for which they had no expertise, a decrease in recruitment of bilateral frontal and parietal regions was observed (Kraeutner et al., 2018). Similarly, when comparing brain activation during MI of a sport-specific skill between novices and the varsity athletes, decreased recruitment of bilateral regions involved in motor planning was observed in the varsity athletes (i.e., the experts; Kraeutner et al., 2018). In contrast, no differences in brain activation patterns were observed when the varsity athletes and novices performed MI of a task for which both groups lacked expertise (Kraeutner et al., 2018). This evidence demonstrates that expertise is reflected in MI-related brain activation (Milton et al., 2007; Chang et al., 2010; Debarnot et al., 2014; Kraeutner et al., 2018), but no conclusions can be drawn in regard to the extent to which practice modality *contributed* to the achieved level of expertise, as the extent to which MI was used to facilitate learning is unknown.

Longitudinal training studies using PP have demonstrated changes in brain activity during MI (Lacourse et al., 2005; Baeck et al., 2012; Bar and DeSouza, 2016). In a task involving shooting, Baeck et al. (2012) demonstrated increased activation in parietal and frontal regions (including the supplementary motor area; SMA) during MI after novices trained with PP. A similar methodology was used with professional dancers acquiring a new dance via PP (Bar and DeSouza, 2016), finding that MI-related activity within the SMA and auditory regions initially increased (i.e., during the early stages of training), but then decreased over the course of training. Lacourse et al. (2005) assessed MI-related brain activation before and after one week of PP of a sequence task, noting an increase in activation localized to frontal and parietal areas following training – areas known to be associated with control of visually-guided actions (Rizzolatti and Matelli, 2003; Culham et al., 2006; Binkofski and Buxbaum, 2013). Additionally, decreased cerebellar and increased striatal activation was found after training, which is a typical pattern for motor learning (Penhune and Doyon, 2002; Doyon and Benali, 2005; Dayan and Cohen, 2011; Censor et al., 2014). As noted earlier, studies that employ only PP during training do not address the question of how the modality of practice used to learn the skill (i.e., MI vs. PP) affects performance outcomes and patterns of brain activity.

There is a body of work examining changes in brain activation following MI-based sequence learning that provides some insight into how the modality of practice used to learn the skill manifests in the resultant brain activity (Jackson et al., 2003; Zhang et al., 2011). MI-related brain activation was assessed before and after MI-based practice of a keypress sequence task (14 sessions; Zhang et al., 2011) and foot sequence task (five sessions; Jackson et al., 2003). Following training, increased activity was observed in regions linked to generating or accessing the mental representation of a movement (in particular, cingulate cortex and precuneus; Zhang et al., 2011) as well as to reward- or familiarity-based response selection (namely orbitofrontal cortex; Elliott et al., 2000; Jackson et al., 2003). One limitation of these studies is the exclusive use of sequence tasks that are limited in the range and complexity of motor skills and thus do not likely generalize to the learning of complex motor tasks. A further limitation is the lack of comparison to patterns of brain activation associated with learning the same task via PP.

To address the limitations of previous research, the present study directly compares changes in brain activity and performance outcomes (i.e., accuracy, consistency, and kinematics) before and after five days of training of a dart throwing task via MI or PP. We hypothesized that for both MI and PP-based training there would be increased activity in cerebellar and contralateral motor regions with the effect being attenuated for MI vs. PP. We hypothesized that performance would improve following both MI- and PP-based training (as demonstrated via increased accuracy and consistency), although these improvements would be less for MI vs. PP. Finally, owing to prior work suggesting differences in the type of encoding that occurs during MI and PP-based learning (Annett, 1995; Frank et al., 2014; Ingram et al., 2016; Kraeutner et al., 2016, 2017; Frank and Schack, 2017) we expected that robust kinematic changes would occur only after training via PP.

3.2 METHODS

3.2.1 Participants

Twenty-four participants (right handed, as determined by a score of ≥40 on the Edinburgh Handedness Inventory (Oldfield, 1971)) were recruited from the local and university community. The Nova Scotia Health Authority research ethics board approved the study. All participants were healthy, reported normal hearing, were free of neurological disorders, had no contraindications to MRI, and each provided written informed consent. All participants engaged in 5 training sessions of the dart throwing task involving either physical practice (PP group) or imagined practice (MI group). All participants underwent fMRI before (pre-training) and after (post-training) the 5 training sessions to obtain brain activity during MI of the dart throwing task.

3.2.2 Experimental Design

At the outset of the experiment, following the informed consent and screening process, participants completed the Motor Imagery Questionnaire - Revised Second Version (MIQ-RS) to characterize each individual’s ability to perform MI (Gregg et al., 2005, 2010). The MIQ-RS is a self-report questionnaire that assesses the vividness and intensity of both the visual and kinaesthetic dimensions of MI, with increasing scores indicative of higher imagery quality (Gregg et al., 2005, 2010).

Each training session (Fig. 3.1) lasted ~20 min, and involved 15 blocks, with six dart throws per block (i.e., a total of 90 dart throws per session, established via prior work examining learning of a dart task (Mendoza and Wichman, 1978; McDonald et al., 1989; Kremer et al., 2009; Spittle and Kremer, 2010; Didier et al., 2013; Querfurth et al., 2016). Dart throwing was performed in accordance with World Dart Federation regulations (World Darts Federation, 2017). Specifically, a competition bristle dartboard was set to regulation height (1.73m from ground to bullseye) and distance (2.37m from throwing line). Participants were instructed to aim at the bullseye and to limit their throws to flexion and extension movements at the elbow in the sagittal plane. Participants performed, or imagined performing, the dart throws (depending on group; PP or MI) with their dominant (right) arm. At the outset of training, participants watched a five min video that familiarized them to the task and provided exemplar performances from male and female performers from both the third and first person perspective.

For the PP sessions, participants threw nickel/brass tipped darts that weighed 22g. Participants were prompted by the experimenter to take a break at the end of each block. For the MI sessions, an auditory script was delivered via noise-cancelling headphones, prompting the participants to imagine picking up the darts and to begin each block when ready. Participants were given 30 sec to complete each block of imagined throws (i.e., similar to the time it took to complete each block of physical throws), with prompts to take a break at the end of each block. At the outset of each MI session, participants were instructed to perform kinaesthetic MI (i.e., first person perspective with an emphasis on the polysensory aspect of the task; Stinear et al., 2006; Schuster et al., 2011) with instructions on how to perform this type of MI provided at the onset of each session.

To obtain our task-related performance outcomes, all participants engaged in a physical test block lasting ~15 min in a pre/post design (Fig. 3.1). Each test block was comprised of 18 dart throws, performed in three blocks of six (similar to parameters employed in Lohse et al., 2010b; Tyč and Boyadjian, 2011; Querfurth et al., 2016). The final location of each dart was digitized (Polhemus Fastrak, Colchester, VT) relative to the board in the order that they were thrown and stored for offline analysis. During the test blocks, video was recorded via a Canon Powershot SX280 HS (Canon Canada, Inc.) mounted on a tripod and placed perpendicular to the throwing line, to capture participant kinematics in the sagittal plane and stored for offline analysis.

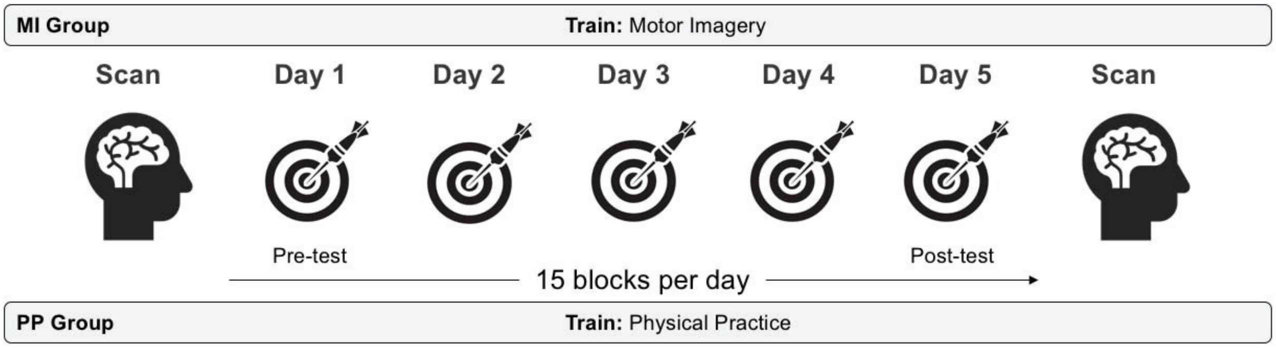


Figure 3.1 Timeline of the experimental design. Participants engaged in five training sessions of either PP or MI-based practice of a dart throwing task. Participants completed two physical testing sessions in a pre/post design (i.e., prior to the start of training on day 1, or following training on day 5), as well as two fMRI sessions pre/post-training to capture changes in brain activation.

Structural and functional MRI data were acquired on a 3 Tesla GE MRI (GE Medical Systems, Waukesha, WI, with a 32 channel RF Head Coil). A 3D T1-weighted anatomical image was acquired using a IR-prepped fast spoiled gradient recalled echo (IR-FSPGR) sequence (inversion time (TI) = 450 ms, repetition time (TR) = 4.0ms, echo time (TE) = 1.33ms, flip angle = 9°, field of view (FOV) 25.6 cm, 256 × 256, 184 sagittal slices at 1 mm thickness, auto-calibrating reconstruction for cartesian imaging

(ARC) phase acceleration = 1, ARC slice acceleration = 1). A T2-weighted anatomical image was acquired using a 3D CUBE sequence (inversion time (TI) = 400 ms, TR = 4200ms, TE = 101 ms, 140 Echo Train Length, 25.6cm FOV, 256 × 256, 184 sagittal slices at 1 mm thickness, ARC phase acceleration = 1.5, ARC slice acceleration = 1). Functional MRI data were acquired using a 2D multi-band echo-planar image (EPI) sequence (TR = 950ms, TE = 30 ms, flip angle = 60°, 21.6 cm FOV, 72 × 72, 3 mm thick slices, 224 volumes, MUX acceleration factor 3 slice direction, ARC acceleration factor 2 in-plane; Stanford Center for Cognitive and Neurobiological Imaging, http://cni.stanford.edu). Additional EPI reference scans with matching parameters except phase-encode blip direction reversal were acquired to facilitate field distortion correction (Andersson et al., 2003; Smith et al., 2004).

The fMRI experiment included four runs performed in a block design. Each run began and ended with a rest block, and included two imagery blocks of the darts task alternating with rest blocks. Each imagery block lasted 28.5 sec, during which participants were asked to imagine performing six dart throws, similar to a single block during the training/testing sessions. The start of each block was cued visually. Participants performed kinaesthetic imagery with their eyes closed, and an auditory tone cued participants to the end of each imagery block. Each rest block lasted 19 sec during which participants were asked to rest quietly with their eyes open. After the completion of each run, participants completed a MI manipulation check where they were asked to rate both their engagement and quality of imagery on a scale of 1 (not engaged; poor quality) to 5 (extremely engaged; excellent quality). Stimuli were delivered using Presentation software (Neurobehavioral Systems, Inc. Berkley, CA), synchronized to MRI data acquisition. Stimuli were presented on a mylar screen positioned across the scanner bore via an LCD projector, which subjects viewed via an angled mirror. Prior to beginning the functional runs, participants were familiarized with the task and type of MI (first person, kinaesthetic) via an auditory script and a 30 sec clip depicting the darts task.

3.2.3 Behavioural analysis

To ensure similarity in the ability to perform MI across groups, MIQ-RS scores were tabulated across participants for each imagery condition (kinaesthetic and visual) and a 2 (imagery condition) X 2 (group) mixed ANOVA was conducted to assess the between group effects of imagery condition on MIQ-RS score. Additionally, responses for both manipulation checks during the neuroimaging sessions were averaged across participants for each run and scan to ensure similarity in imagery performance across groups. Separate 2 (time point) X 2 (group) mixed ANOVAs were conducted on each outcome measure (engagement, quality) to assess the between group effects on task engagement and imagery quality.

Performance was measured in terms of accuracy (mean radial error; MRE) and consistency (bivariate variable error; BVE; Hancock et al., 1995; Edwards et al., 2007; Lohse et al., 2010b; Schorer et al., 2012; Sherwood et al., 2014; Querfurth et al., 2016). As our measure of accuracy (MRE), does not capture directional information, we did not provide this information as a form of feedback to our participants (i.e., in addition to the visual feedback they received after each physical dart throw). For the above noted outcome measures, the bullseye was considered the point of origin (0,0) and deviations in the X and Y plane from the point of origin were obtained from the digitized data. The first throw of each block during the test sessions was considered warm-up and omitted from further analyses (i.e., leaving 15 total throws per test session). For both performance and kinematic outcomes, outliers were identified as throws that exceeded three standard deviations above the mean for each participant across sessions and were removed from further analyses.

Video data were analyzed using Dartfish Pro motion analysis software (Dartfish HQ, Fribourg, Switzerland) to derive shoulder angle, elbow angle, throwing time, and preparation time (Lohse et al., 2010b; Sherwood et al., 2014). Shoulder and elbow flexion angles were measured at the point of maximum elbow flexion (i.e., also termed the 'take back') and the point of release for each dart throw, with anatomical markers placed on the acromion process, olecranon, and highest point of the iliac crest in line with the coronal plane of the body (for shoulder angle) or styloid process of the throwing arm (for elbow angle). Throwing time was defined as the time between maximum elbow flexion to the point of release. Preparation time was defined as the time between the point of release to maximum flexion of the subsequent throw. Mean and SD values are reported for these kinematic variables, but like Lohse et al., (2010b) only SD (calculated across trials per test session for each participant) was used in the group-level analyses (described below) as we were interested in assessing changes in kinematic variability. Angular velocity, defined as the angle at maximum flexion subtracted from the point of release and divided by the throwing time, was also calculated (Lohse et al., 2010b). For angular velocity, we assessed changes in the absolute values (i.e., mean values) instead of its variability for each group, consistent with prior literature suggesting that increased angular velocity is associated with expert performance of throwing tasks (Hansen et al., 2012), and that precision of speed is a critical factor underlying throwing consistency in darts (Smeets et al., 2002).

Mean values for the above noted performance-related outcome measures and SD for each kinematic variable was determined for each participant at each test session (pre/post). Separate 2 (group) X 2 (time point) mixed ANOVAs were conducted for each measure to assess the between-group effects of training. Prior to statistical analyses, all data were tested for normality and homogeneity of variance using Shapiro-Wilk and Bartlett's tests. Data that did not meet the assumptions of ANOVA were analyzed using non-parametric tests. Effect sizes were calculated within each group (i.e., between test sessions) for each outcome measure to characterise the extent to which performance improved over the course of training. All statistical analyses were performed using R (R project for statistical computing) with an a priori alpha of 0.05 denoting significance.

3.2.4 fMRI preprocessing and analysis

Preprocessing and statistical analyses were performed using the Oxford Centre for Functional MRI of the Brain's (FMRIB) software library (FSL v.5.0.10; FMRIB Oxford, www.fmrib.ox.ac.uk/fsl) and fMRI Expert Analysis Tool (FEAT) version 5.0.10 (Smith et al., 2004; part of FSL). Preprocessing of the anatomical T1 and T2 scans included registration based skull-stripping to template brain MNI152_T1_1mm using FLIRT and FNIRT.

fMRI preprocessing included motion correction with MCFLIRT (Jenkinson et al., 2002), field inhomogeneity-induced distortion correction with reverse-phase encoded blips using TOPUP (Andersson et al., 2003), brain extraction using BET (Smith et al., 2002), spatial smoothing using a Gaussian kernel (FWHM 5mm), and high-pass temporal filtering at 0.01 Hz to remove low-frequency noise. Functional images were then rigid-body spatially co-registered (using 6DOF) to the processed anatomical image using FLIRT and combined with the non-linear registration to MNI152_1mm with a voxel size of 3mm for group comparison of individual fMRI results.

Individual statistical activation maps were calculated within each run using a general linear model (GLM) with FEAT with motion outliers included as confounds, determined from a contrast of imagery (darts) vs. rest computed for each run (first-level analysis). A second-level analysis combined all runs in a fixed effects model to produce contrast of parameter estimate (COPE) maps for each individual and time point (pre/post).

High-level group analyses were carried out using FLAME (FMRIB's Local Analysis of Mixed Effects) model with FEAT. All analyses used a corrected cluster threshold of $Z > 2.0$ and significance threshold of $p < .05$, corrected for family-wise error. To assess the impact of training modality on resultant patterns of MI-related brain activity, a between-group comparison was conducted on the averages of the lower-level COPE maps for each group at the post-training scan, with a performance outcome (BVE) added as a covariate to account for resultant differences in performance across participants regardless of equal practice of the task. We adjusted for BVE as consistency is shown to be a more stable measure than accuracy and less influenced by external factors (e.g., time-of-day, fatigue; Edwards et al., 2005, 2007; Kumar et al., 2017). To characterise changes in brain activation driven by each modality of training, averages of the lower-level COPE maps for each time point were compared within-groups.

3.3 RESULTS

Two participants were excluded from the study (one from the MI group because they did complete the first MRI session and subsequently dropped out; and one from the PP group for excess head motion during scanning that exceeded our exclusion criteria of 2.0 mm), leaving 22 participants (PP group: $n = 11$, 8 female; aged 24.6 ± 4.7 years; MI group: $n = 11$, 7 female; aged 24.5 ± 4.2 years) for the final analyses. Further, one participant from the MI-PP group had only engaged in two of the three blocks during each testing session. Both groups demonstrated similar MI ability, evidenced by MIQ-RS scores in both the visual and kinaesthetic imagery conditions (Table 3.1). Neither the main effect for group ($F_{1,20} = 3.34$, $p = 0.08$) or imagery condition ($F_{1,20} = 0.33$, $p = 0.57$) was significant, and the interaction between group and imagery condition was not significant ($F_{1,20} = 0.67$, $p = 0.42$). Engagement in, and quality of, imagery was also similar between groups at both time points, as evidenced by responses to our manipulation checks during both neuroimaging time points (Table 3.1). For engagement, neither the main effect for group ($F_{1,20} = 0.13$, $p = 0.72$) or time point ($F_{1,20} = 0.74$, $p = 0.40$) was significant, and the interaction between the two was also not significant ($F_{1,20} = 1.28$, $p = 0.27$). For quality, neither the main effect for group ($F_{1,20} = 1.81$, $p = 0.19$) nor time point ($F_{1,20} = 0.003$, $p = 0.96$) was significant, and the interaction between the two was not significant ($F_{1,20} = 0.68$, $p = 0.42$).

3.3.1 Performance outcomes

Means and standard deviations for MRE and BVE are reported in Table 3.2. As data for MRE and BVE did not meet the assumptions of ANOVA, separate Kruskal-Wallis rank sum tests were conducted to analyze the between-group effects at each time point, followed by effect sizes calculated within each group (i.e., between test sessions) to characterise improvements in performance as previously stated. No between-group differences existed for MRE ($H = 0.14$, $p = 0.71$) or BVE ($H = 0.02$, $p = 0.88$) at the pre-test. BVE differed between the PP and MI group at the post-test ($H = 4.6$, $p = 0.03$), with a trend towards significance for MRE ($H = 3.5$, $p = 0.06$). Effect sizes revealed a moderate (MRE) and large (BVE) effect of training within the PP group (Table 3.2). Within the MI group, no difference was noted when comparing MRE across time points, however a small effect for BVE indicated an improvement in consistency as a result of training (Table 3.2).

Means and standard deviations for the kinematic variables are reported in Table 3.2. With the exception of angular velocity, the kinematic data did not meet the assumptions of ANOVA, and therefore separate Kruskal-Wallis rank sum tests were conducted to analyze between group effects at each time point (Table 3.3). No significant differences between groups at either time point were observed. The 2 (group) x 2 (time point) ANOVA conducted on angular velocity (°/sec) revealed no main effect of group [F(1,19) = 0.41, *p* = 0.528] and no significant interaction [F(1,19) = 0.55, *p* = 0.466]. However, a significant main effect of time point was observed [F(1,19) = 8.08, *p* = 0.010], indicating that angular velocity increased after training regardless of modality. Effect sizes, calculated to characterise the change in variance across sessions as stated above, revealed a decrease in kinematic variability in the PP group from pre- to post-test across all of our variables of interest, with the exception of elbow angle at the point of release and preparation time (Table 3.3). However, only kinematic variability of the shoulder angle at maximum flexion, preparation time, and angular velocity showed meaningful changes from pre- to post-test in the MI group (Table 3.3).

Table 3.1

MIQ-RS scores and manipulation check ratings (mean and SD for each group).

		Group	
		MI	PP
MIQ-RS score	Kinaesthetic (/49)	35.6 (12.0)	38.7 (8.1)
	Visual (/49)	38.7 (8.3)	39.9 (7.3)
MI engagement (/5)	Scan 1	4.3 (0.7)	4.3 (0.5)
	Scan 2	4.3 (0.7)	4.1 (0.6)
MI quality (/5)	Scan 1	4.2 (0.7)	4.0 (0.7)
	Scan 2	4.3 (0.6)	3.9 (0.6)

Table 3.2

Behavioural data (mean and SD) for performance outcomes and kinematic variables of interest. Effect sizes conducted to characterise changes in performance (day 1 minus day 5) are included. A negative effect size reflects a decrease in error (MRE and BVE), and a decrease in kinematic variance (calculated using the SD of each kinematic variable) across practice sessions.

			Group					
			MI			PP		
			Day 1	Day 5	*d*	Day 1	Day 5	*d*
Mean Radial Error (cm)			8.70	8.93	0.05	8.04	5.96	-0.69
			(3.89)	(5.08)		(4.05)	(1.41)	
Bivariate Variable Error (cm)			9.69	8.58	-0.26	9.19	5.72	-0.97
			(4.72)	(3.84)		(4.92)	(1.24)	
Kinematic Variable								
Shoulder (°)	Flexion	Maximum	63.0	65.7	-0.61	68.0	70.8	-1.01
			(4.4)	(3.3)		(5.2)	(2.8)	
		Release	80.4	80.8	0.09	82.8	85.3	-0.39
			(5.3)	(5.7)		(4.5)	(3.9)	

Elbow (°)	Maximum	36.2	36.9	0.24	35.5	38.0	-0.36
	Flexion	(2.6)	(2.8)		(3.1)	(2.7)	
	Release	92.4	96.1	-	96.9	95.2	-0.18
		(13.4)	(12.9)	0.16	(11.9)	(11.2)	
Time (sec)	Preparation	4.37	4.50	-	3.70	3.52	-0.04
		(1.45)	(1.25)	0.32	(0.91)	(0.89)	
	Release	0.176	0.170	-	0.205	0.158	-0.46
		(0.028)	(0.027)	0.07	(0.032)	(0.026)	
Angular Velocity[†] (°/ sec)		329.8	365.6	0.35	289.1	350.9	0.55
		(86.8)	(70.5)		(69.8)	(73.2)	

[†] Note: effect sizes calculated for angular velocity were conducted on the mean values observed for day 1 and day 5, and thus a positive effect size is indicative of an increase in angular velocity across practice sessions.

Table 3.3

Kruskal-Wallis rank sum tests conducted to analyze the between group effects on kinematic variability (i.e., on the resultant SD values) at each time point.

Kinematic Variable		Day 1		Day 5	
		H	*p*	*H*	*p*
Shoulder Flexion	Maximum	0.6	0.439	2.4	0.121
	Release	0.179	0.673	0.972	0.324
Elbow Flexion	Maximum	0.714	0.398	0.005	0.944
	Release	1.46	0.23	0.50	0.481
Time	Preparation	1.98	0.159	1.79	0.181
	Release	1.12	0.291	0.011	0.916

3.3.2 fMRI

Table 3.4 reports the MNI coordinates of activation observed for between-group comparisons, accounting for BVE. To identify a priori group differences in MI-based brain activation we initially compared activation maps between groups for the pre-training scan. Greater activation, localized to the ipsilateral cerebellum, was observed for the MI group (MI > PP; Table 3.4). Between-group comparisons at the post-training scan, accounting for BVE, revealed greater activation for the PP group (PP > MI), localized to regions including the SMA, anterior cingulate cortex, cerebellum, contralateral precentral and middle temporal gyri, and ipsilateral superior frontal gyrus (Fig. 3.2). No increases in activation were observed for the MI group relative to the PP group (i.e., MI > PP). Negative correlations between BVE and MI-related activity were found in regions including bilateral parietal cortices and lingual gyri (Table 3.4; Fig. 3.3).

Table 3.5 reports the MNI coordinates of activation resulting from within-group comparisons. Within-group comparisons revealed greater activation in contralateral anterior cingulate cortex and middle temporal gyrus, ipsilateral inferior parietal lobule (localized to the supramarginal gyrus), and bilateral medial orbitofrontal cortex within the PP group when comparing the post- to pre-training scans (post > pre-training; Table 3.5). No decreases in activation were observed (pre > post-training) for the PP group. No significant differences in activation were observed from pre- to post-training within the MI group. Prior to conducting group-level comparisons, we generated a MI vs. rest (i.e., task-positive) activation map across all participants for the pre-training scan, demonstrating activation in a number of regions typically activated during MI, including bilateral frontal, contralateral precentral gyrus, and ipsilateral cerebellar regions (Hétu et al., 2013; Hardwick et al., 2018). This data is included as Supplementary Materials (Appendix B; Figure 6.2).

Table 3.4

MNI coordinates of local maxima resulting from between-group comparisons conducted at each time point.

Anatomical Region			MNI coordinates (mm)			Z-score
			x	y	z	
Pre-training						
	MI > PP	R Cerebellum (lobule VI)	24	-59	-34	3.25
		R Cerebellum (lobule VIIb)	26	-77	-47	3.38
		R Cerebellum (lobule VIIb)	33	-69	-47	3.08
		R Cerebellum (lobule VIII)	22	-59	-37	3.13
		R Cerebellum (crus I)	39	-88	-32	2.85
		R Cerebellum (crus II)	28	-90	-40	3.12
	PP > MI	-	-	-	-	-
Post-training						
	MI > PP	-	-	-	-	-
	PP > MI	L Superior temporal pole	-36	27	-26	3.73
		L Middle temporal gyrus	-67	-10	-2	3.53
		L Superior temporal pole	-46	3	-15	3.4
		L Middle temporal gyrus	-64	-12	-7	3.33
		L Superior temporal pole	-55	12	-10	3.27
		L Superior temporal pole	-56	9	-7	3.27

	L Cerebellum (lobule VI)	-26	-59	-29	3.22
	L Cerebellum (lobule VI)	-27	-62	-20	3.1
	L Cerebellum (lobule IV/V)	-4	-59	-18	3.06
	L Anterior cingulate	0	8	26	3.39
	L Medial frontal gyrus	-11	34	35	2.81
	L Anterior cingulate	-9	33	18	2.73
	L Precentral gyrus	-30	-16	76	3.23
	L SMA	-11	-5	73	3.22
	L SMA	-8	0	81	3.21
	L Paracentral lobule	-16	-20	77	3.13
	R Cerebellum (lobule IV/V)	10	-46	-7	3.2
	R Cerebellum (vermis IV/V)	4	-58	-16	3.1
	R Cerebellum (lobule IV/V)	11	-50	-7	2.93
	R Anterior cingulate	10	12	30	2.81
	R SMA	2	-3	58	2.73
	R SMA	2	3	52	2.71
	R Superior frontal gyrus	16	-3	74	3.11
	R Superior frontal gyrus	27	-5	68	3.0
Positive BVE effect	-	-	-	-	-
Negative BVE effect	L Superior parietal lobule	-18	-51	51	3.52
	L Superior parietal lobule	-17	-51	53	3.51

L Precuneus	-18	-51	51	2.91
L Lingual gyrus	-8	-59	53	3.34
L Lingual gyrus	-19	-78	0	3.32
L Lingual gyrus	-21	-78	1	3.32
L Lingual gyrus	-21	-80	0	3.31
L Calcarine	-20	-74	0	3.07
R Superior parietal lobule	21	-66	64	3.45
R Angular gyrus	40	-60	30	3.32
R Superior parietal lobule	27	-56	66	3.02
R Lingual Gyrus	19	-77	-1	3.05

Note: instances in which no significant differences in activation were noted are indicated by dashed lines.

Table 3.5

MNI coordinates of the local maxima resulting from comparisons conducted to assess within-group differences in MI-related brain activation following training of the dart throwing task.

Anatomical region		MNI coordinates (mm)			Z-score
		x	y	z	
PP-group					
Post > pre	L Middle temporal gyrus	-66	-14	-4	4.51
	L Thalamus	-4	-20	-7	4.38
	L Middle temporal gyrus	-62	-4	-8	4.34
	L Anterior cingulate	-14	49	-3	3.54
	L Middle frontal gyrus (orbital)	-18	57	-16	3.53
	L Medial orbitofrontal cortex	-10	56	-1	3.36
	R Supramarginal gyrus	44	-39	22	4.53
	R Supramarginal gyrus	46	-39	24	4.45
	R Supramarginal gyrus	49	-39	25	4.43
	R Medial frontal gyrus	6	38	54	3.65
	R Medial orbitofrontal cortex	9	59	0	3.51
	R Medial frontal gyrus	15	49	2	3.46
Pre > post	-	-	-	-	-
MI-group					
Post > pre	-	-	-	-	-

	Pre > post	-	-	-	-	-

Note: instances in which no significant differences in activation were noted are indicated by dashed lines.

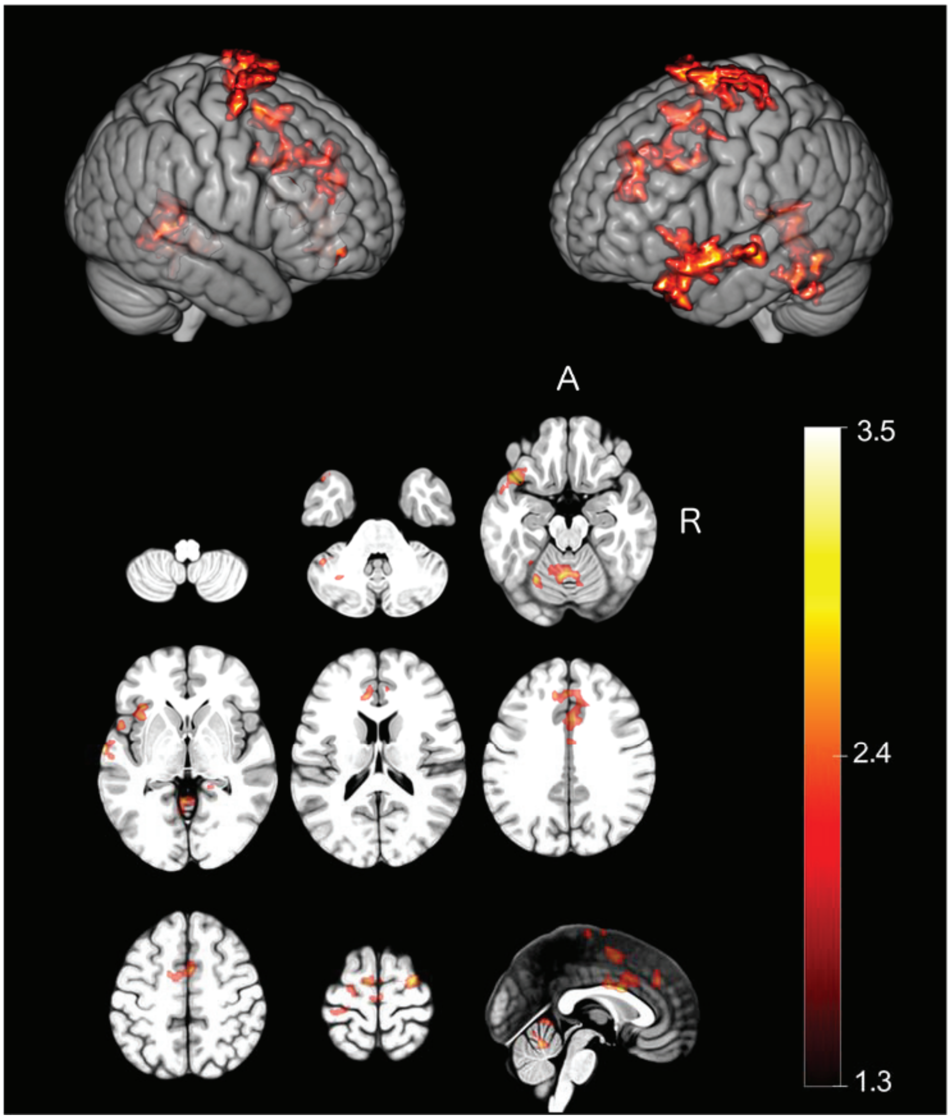


Figure 3.2 Differential effects on resultant MI-based brain activity following training after PP vs. MI where the colourbar represents the Z-max value. Activated voxel clusters remaining after subtraction of the map of activations of the MI group from the PP group, accounting for BVE. Activation localized to regions including supplementary motor area (SMA), anterior cingulate cortex, cerebellum, contralateral precentral and middle temporal gyri, and ipsilateral superior frontal gyrus. Only clusters are shown that reached a cluster corrected threshold ($Z>2.0$; $p < 0.05$), family-wise error corrected for number of comparisons, and are shown overlaid on the MNI template. Note: no activated voxel

clusters remained after subtraction of the activation map of the MI group from the PP group, and thus this difference map is not shown.

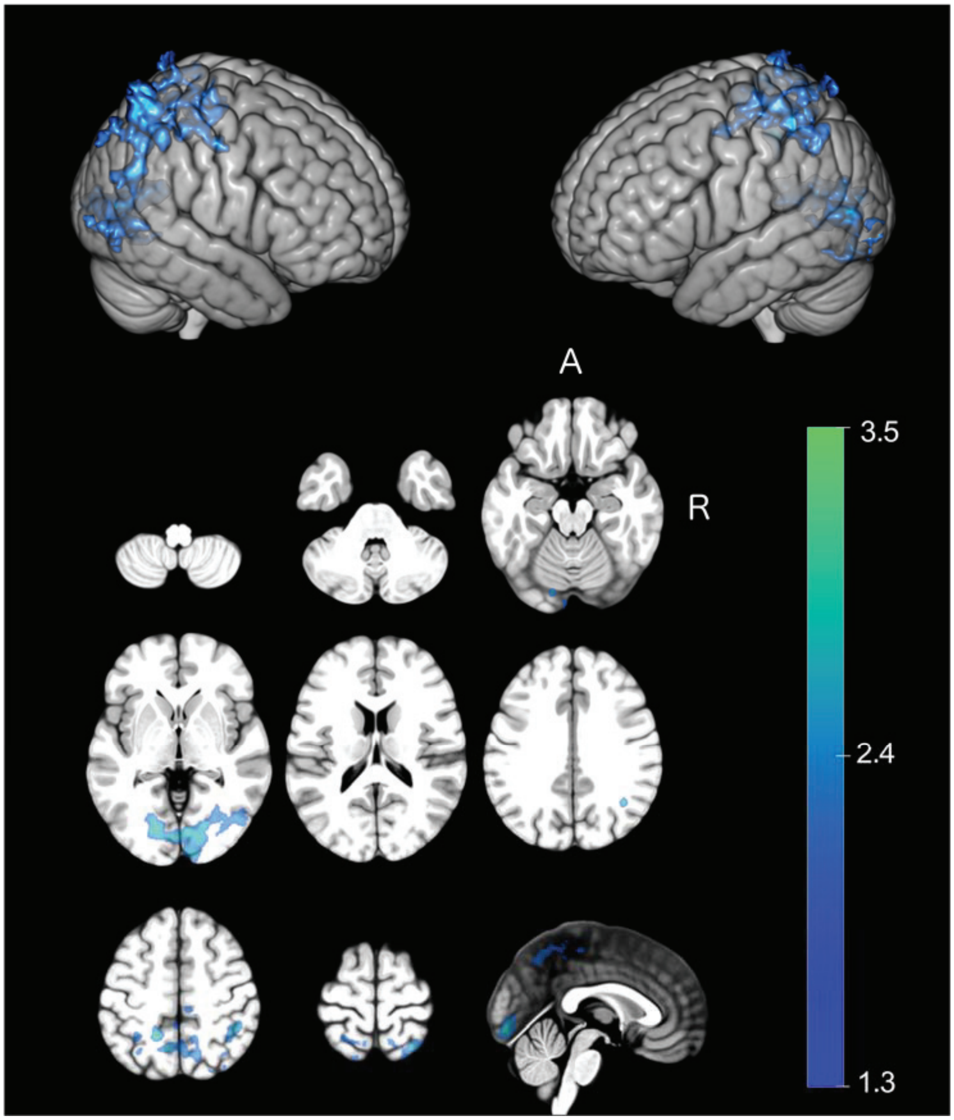


Figure 3.3 Correlation between brain activity and performance, where the colourbar represents the Z-max value. During MI, BVE correlates negatively with brain activity localized to bilateral parietal cortices and lingual gyri. No positive correlations were observed and are thus not shown. Only clusters are shown that reached a cluster corrected threshold ($Z>2.0$; $p < 0.05$), family-wise error corrected for number of comparisons, and are shown overlaid on the MNI template.

3.4 DISCUSSION

The current study sought to determine how the modality of practice used to learn a complex motor skill manifests in the pattern of MI-based brain activity and performance. Contrary to our hypotheses, no significant increases in brain activation were driven by MI-based practice. Consistent with our hypotheses, greater brain activation localized to cerebellar and contralateral areas within the motor network were observed following equivalent amounts of training via PP vs. MI. Further, as hypothesized, the degree of improvements in performance driven by MI-based practice was inferior to those achieved via PP. Below we discuss our findings in the context of prior work examining MI-based brain activation and the neural networks underlying expertise.

3.4.1 Modality-specific differences

By directly comparing an equal amount of MI- or PP-based training of a complex motor skill, our findings provide novel evidence that the modality used to facilitate learning modulates brain activation patterns observed during MI of the skill. We observed greater activation in the PP vs. MI group at the post-training scan, encompassing the SMA and cerebellum bilaterally, left primary motor cortex (i.e., precentral gyrus), the anterior cingulate cortex, and frontal regions including the left medial frontal gyrus and right superior frontal gyrus – regions known to be active during MI (Hanakawa et al., 2008; Burianová et al., 2013; Hétu et al., 2013; Kraeutner et al., 2014; Hardwick et al., 2018) and to underlie skilled motor performance and control (Rizzolatti et al., 1998, 2014; Dayan and Cohen, 2011; Binkofski and Buxbaum, 2013; Hardwick et al., 2013). Further, our results indicate that unlike PP, brain activation patterns did not undergo significant change following MI-based practice. Coupled with the similarity observed between groups prior to initiating training, our findings suggest that MI training alone is not sufficient to drive changes in brain activation that manifest in improved performance, in a manner similar to PP, as one moves along the continuum from novice to expert.

Our behavioural results show that despite both groups engaging in the same amount of training, performance improvements in MI were marginal relative to that observed for PP. MI-based training did not result in improved accuracy, driving only small changes in consistency (albeit to a lesser extent than PP, as noted by a small vs. large effect size) and kinematics. In contrast, robust changes in accuracy and consistency were observed after PP-based training, as well as a consistent decrease in variability across the kinematic outcomes. Why MI did not result in more impressive changes closer to the magnitude observed for PP is attributable to fundamental differences between the two modalities. Building on prior work in the area Wohldmann et al., 2007; Lohse et al., 2010a; Frank et al., 2015; Ingram et al., 2016, 2019; Land et al., 2016; Frank and Schack, 2017; Kraeutner et al., 2017), we propose two explanations for our findings: 1) that refinement of the motor program is less robust in MI owing to a difference in the mechanism underlying learning; and 2) that different information is encoded in MI relative to PP.

In MI, unlike PP, the absence of sensory information about task performance (i.e., reafference) likely impairs the error detection/correction process that is needed to trigger changes to the motor program. This notion is supported by the observation of greater SMA and cerebellar activation following PP- but not MI-based training. It is well established that the SMA is a key substrate in motor planning and execution (Tanji and Kurata, 1982; Tanji and Shima, 1996; Nachev et al., 2008; Dayan and Cohen, 2011; Flash and Bizzi, 2016) and increased SMA activity is observed as long-term learning occurs (Dayan and Cohen, 2011). For instance, Tanji and Kurata (1982) showed that output of both SMA and primary motor cortex neurons increases prior to movement onset in primates. Yet, SMA activity was shown to precede primary motor cortex activation (i.e., there was a weaker correlation between SMA output and reaction time of the animal relative to the primary motor cortices; Tanji and Kurata, 1982), indicating that the SMA generates a preparatory state for the impending (and forthcoming) movements, ultimately relaying the motor command to the primary motor cortices for output to the effectors (Roland et al., 1980; Tanji and Kurata, 1982; Tanji and Shima, 1996; Cunnington et al., 2005). Throughout motor skill acquisition, output of cerebellar neurons is modulated by discrepancies between predicted and feedback representations in internal models (Brooks and Cullen, 2013), whereby the predicted consequences of the movement (efference copy) are compared to actual movement outcomes (reafference) in a forward model to update the motor program (Miall and Wolpert, 1996; Wolpert et al., 1998; Bastian, 2006; Popa et al., 2012). Integral in error detection/correction, it follows that increases in bilateral cerebellar activation are typically observed in early (i.e., 'fast') stages of motor learning when error magnitude is large and substantial alterations to the motor program are made (Seitz et al., 1994; Ungerleider et al., 2002; Lacourse et al., 2004; Doyon and Benali, 2005; Dayan and Cohen, 2011). The lack of significant SMA and cerebellar activity following MI-based training (relative to PP) does not necessarily indicate that a similar error detection/correction mechanism is not at work. While not large in magnitude, participants in the MI group did realize changes in performance as a result of training. Recent work aids in the explanation of these findings: MI is theorized to rely on a forward model, with a mechanistic difference being that an alternative internal comparison may be occurring in which the predicted consequences of the movement are compared to a simulated representation of the movement that may produce a corresponding sensory representation (O'Shea and Moran, 2017; Kilteni et al., 2018; Ingram et al., 2019). In this scenario, it is likely that any discrepancy observed between the predicted consequences and simulated feedback representation is much smaller than that which occurs when feedback is derived from actual sensory information. Given that the discrepancy between predicted consequences and simulated feedback is minimal, reliance on the cerebellum for error detection/correction is lessened as only marginal alterations to the motor program are made, and improvements in performance as a result are diminished.

Importantly, recent work from our lab and others suggests that the motor program undergoes training-related alterations during MI-based practice (Gentili et al., 2006, 2010; Kraeutner et al., 2016b; Ingram et al., 2019). In other words, motor learning occurred in the absence of sensory feedback. For instance, in employing a multi-articular tracing task over five sessions, Ingram and colleagues (2019) showed that MI-based practice facilitated improvements in performance that while smaller in magnitude relative to PP, were greater than that observed for PP without visual feedback (Ingram et al., 2019). The authors hypothesized that MI-based learning does not depend on sensory feedback and instead occurs through an alternative mechanism (such as an alternate forward model process, as described above; Ingram et al., 2019), where feedback is simulated. Coupling the present neuroimaging results with the oft-observed finding of performance improvements that are inferior in comparison to PP (including the present work), we suggest expertise of a complex motor skill cannot be achieved through MI-based practice alone, or at the very least, the process is slowed. Specifically, robust improvements in performance are not realized because MI is missing the richness of the sensory feedback (that results from overt execution) such that insufficient updates to the motor program are made within each bout of practice. It may well be that a proportionately larger amount of MI-based training would result in performance improvements and coincident changes in brain activation patterns akin to those driven by PP, although this is as yet an unexplored area of research.

The second explanation for our findings relates to the type of information that is encoded between the two modalities. A growing body of evidence suggests that MI differs from PP in that only global vs. specific aspects of the movement are encoded as a result of MI-based training (Annett, 1995; Frank et al., 2014; Ingram et al., 2016; Kraeutner et al., 2016a, 2017; Frank and Schack, 2017). Specifically, MI is theorized to facilitate effector independent (i.e., global or abstract features) vs. dependent encoding (movement parameters specific to an effector) (Mizuguchi et al., 2014; Ingram et al., 2016; Kraeutner et al., 2016a, 2017; Land et al., 2016). In line with this argument, we observed greater activation in the contralateral primary motor cortex, critical for effector dependent encoding and mapping the motor program to the specific effector, in the PP vs. MI group post-training, which may reflect a lack of effector dependent encoding occurring via MI-based practice. In line with this thinking, work employing inhibitory brain stimulation has demonstrated the critical role of posterior parietal regions, implicated in effector independent encoding, in MI (Lebon et al., 2012; Evans et al., 2016; Kraeutner et al., 2016a, 2019). In contrast, inhibition of the primary motor cortices did not affect MI-based learning of a sequence task (Kraeutner et al., 2017), and activation of the primary motor cortex during MI is inconsistent in the literature (Hétu et al., 2013; Hardwick et al., 2018). Further, consistency, preparation time, and angular velocity – our primary changes in performance associated with MI-based training – are global aspects of a movement that may improve with effector independent encoding, regardless of effector dependent encoding. Additionally, previous research suggests the SMA is the neural substrate implicated in transforming desired kinematics to be used in the task to the set of forces exerted by the effectors (termed the ‘kinematics-to-dynamics transformation’; Li et al., 2001; Padoa-Schioppa et al., 2002, 2004). Due to the covert nature of MI (i.e., the movement is not actually performed), the dynamics of the movement are likely not being encoded. Accordingly, the lack of SMA activation observed in the MI group post-training relative to PP likely indicates that no kinematics-to-dynamics transformations were occurring in the MI group. It follows then that perhaps MI was only able to drive changes in these performance outcomes because of their global nature. How the mechanistic differences underlying MI- vs. PP-based training impacts behavioural outcomes achieved at different stages of learning represents an important avenue for future research.

3.3.2 Expertise and MI-related brain activation

Our findings also extend prior work examining how expertise modulates MI-based brain activation. As previously mentioned, evidence generated primarily from cross-sectional studies has shown that MI-based brain activation associated with novice vs. expert performance is more diffuse, resulting in the additional recruitment of bilateral regions (Milton et al., 2007; Chang et al., 2010; Debarnot et al., 2014; Kraeutner et al., 2018). However, these studies do not control for the modality in which the expertise was achieved, nor do they permit the amount of training (across the experts) to be controlled for. Here, while none of our participants achieved an expert level of proficiency with the dart throwing task, we showed that improvements in performance after a controlled amount of training, regardless of modality, were negatively correlated with activation encompassing bilateral posterior parietal regions and visual regions (localized to lingual gyri and calcarine sulci). This finding is in alignment with prior work: additional recruitment of bilateral posterior parietal regions is shown to associated with novice performance, when experts performed imagery a novel task vs. their sport-specific skill (Kraeutner et al., 2018), and experts vs.

novices performed imagery of their sport specific skill (Milton et al., 2007), and novices demonstrated greater activation in parietal and visual areas relative to experts during MI of a high jump (Olsson et al., 2008; Olsson and Nyberg, 2010). As posterior parietal regions are critical to movement planning and visuospatial processing necessary for skilled movement (Rizzolatti et al., 1998; Rizzolatti and Matelli, 2003; Binkofski and Buxbaum, 2013; Rizzolatti et al., 2014) it follows that these regions are heavily relied on during novice performance.

Specifically, in order to first generate an initial motor representation of the skill to be learned, there is a greater reliance on posterior parietal areas that become less involved as learning occurs and the motor program is refined (Olsson et al., 2008b; Olsson and Nyberg, 2010; Dayan and Cohen, 2011). Coinciding with the reliance of posterior parietal areas critical to generating and establishing the motor representation, as suggested by Olsson et al. (2008a), novices likely create a ‘new’ image of the skill as there is no existing motor representation to access or rely on. Thus, at the outset of training, novices more heavily recruit visual areas vs. motoric pathways. Indeed, recruitment of visual areas during MI is typically linked to visual but not kinaesthetic imagery (Solodkin, 2004; Hétu et al., 2013). Here, the absence of changes in brain activation from pre- to post-training in the MI group may therefore reflect that these participants were still relying on a visual image at the post-training scan, while the observed differences in brain activation pre/post in the PP group may reflect the ability to rely on the now-established motor representation after training in this modality. Of note, that we did not observe statistically significant changes in SMA and cerebellar regions in our within-group analyses is likely due in part to our participants performing MI in the scanner (i.e., in that no kinematics-to-dynamics transformation is occurring as no motor command is being output to the effectors), or that these increases may only occur after longer term practice, as shown in Bar and De Souza (2016). In light of the current findings, an individual who performs MI of a skill they are naïve to likely relies on a visual image (or a visual imagery strategy) until enough learning has occurred to activate motor pathways and properly perform kinaesthetic imagery.

3.4.3 MI training

A question arising from general investigations of MI is the notion that MI is a skill in and of itself. One may therefore postulate that by engaging in MI-based training of the dart throwing task, the individual's ability to perform MI and thus recruit neural substrates within the motor network during MI is increasing. Under this assumption, the associated changes of brain activation observed in the current study and prior work may reflect improvements in MI ability. In this context, stemming from prior work demonstrating that brain activation patterns of MI and PP of the same task converge following a bout of MI-based training (Lacourse et al., 2005), and that increasingly lateralized activity is associated with MI of a task with the provision of real-time neurofeedback during MI-based training (i.e., in that the individual is given feedback about the quality of their imagery performance vs. task-related feedback; Boe et al., 2014), we would expect that the MI group would thus show an increasingly focal pattern of brain activity. Contrary to this prediction, that we did not observe within-group changes in the MI group, taken in conjunction with the between-group comparisons resulting in differences localized to regions within the motor network, suggests that any differences in brain activation were indeed associated with task specific changes as opposed to changes in the 'task' of doing MI. However, future work is required to examine the longitudinal effect of generalized MI training (i.e., such as via layered stimulus response training, to develop different imagery processes, as suggested in (Cumming and Eaves, 2018; Eaves et al., 2018) on resultant MI-based brain activity.

3.4.4 Limitations

As prior work employing sequence tasks has demonstrated changes in brain activity driven by MI-based training, it is important to consider why we did not observe robust changes in MI-related brain activation following five days of MI-based training. As indicated by Dayan and Cohen (2011), the stages of learning depend on the nature of the task. In particular, the fast stage of learning of a sequence task may persist for a number of minutes (Dayan and Cohen 2011), resulting in a robust change in brain activation after multiple sessions that indicate a shift to the slow stage of learning (Jackson et al., 2003; Zhang et al., 2011). In contrast, we employed a multi-articular complex motor skill whereby the fast stage of learning may persist for a number of months (Dayan and Cohen 2011). Here, participants were likely still in the early stages of learning at the post-training scan (evidenced by imperfect accuracy and consistency at the post-test, regardless of improvements in performance in either group). In the MI group however, the associated lack of changes in brain activation driven by five days of training via MI are supported with the minimal differences observed across our performance outcome measures – robust learning did not occur in the MI group. Alternatively, methodological limitations associated with fMRI should also be taken into consideration. While BOLD is (indirectly) reflective of an increased use of neural substrates, fMRI is limited by its low temporal resolution and the ability to measure direct electrophysiological activity (Sutton et al., 2009). Thus, while neuronal activity is upregulated during repeated MI-based practice, resulting in lasting changes in the activation pattern during MI of that task (Jackson et al., 2003; Zhang et al., 2011), evidence from direct electrophysiological measures has shown that the extent to which neuronal upregulation occurs is less than that of PP and these changes may therefore go undetected by fMRI. In particular, studies employing magnetoencephalography and electroencephalography to compare MI- and PP-based brain activation on a millisecond-by-millisecond basis of the same task have shown that the magnitude of activity driven by MI is reduced relative to PP in regions associated with skilled motor practice, and sustained for a shorter duration (Burianová et al., 2013; Kraeutner et al., 2014; Duann and Chiou, 2016). Consequently, while upregulation of neuronal activation may occur as learning is facilitated via MI, the change in activation may be too minimal or not sustained long enough to be observed via fMRI (Pfurtscheller and Neuper, 1997; Kraeutner et al., 2014).

3.4.5 Conclusion

Here, we showed that relative to PP, MI-based training did not drive robust changes in brain activation and was inferior for realizing improvements in performance: greater activation in regions critical to refining the motor program were observed in the PP vs. MI group post-training, and MI led to smaller improvements in performance relative to PP. Together, extending prior work related to the mechanisms underlying learning via MI-based practice, our findings indicate that 1) refinement of the motor program is less robust in MI owing to a difference in the mechanism underlying learning, and 2) different information is encoded in MI relative to PP. Ultimately, the current study provides unique knowledge regarding how the modality of practice (i.e., MI vs. PP) used to learn a complex motor skill manifests in resultant patterns of brain activity, as well as differences in performance.

3.5 REFERENCES

Andersson J, Skare S, Ashburner J (2003) How to correct susceptibility distortions in spin-echo echo-planar images: application to diffusion tensor imaging. Neuroimage 20:870–888.

Annett J (1995) Motor imagery: perception or action? Neuropsychologia 33:1395–1417.

Baeck J-SS, Kim Y-TT, Seo J-HH, Ryeom H-KK, Lee J, Choi S-MM, Woo M, Kim W, Kim JG, Chang Y (2012) Brain activation patterns of motor imagery reflect plastic changes associated with intensive shooting training. Behav Brain Res 234:26–32.

Bar RJ, DeSouza JF (2016) Tracking Plasticity: Effects of Long-Term Rehearsal in Expert Dancers Encoding Music to Movement. PLoS ONE 11:e0147731.

Bastian AJ (2006) Learning to predict the future: the cerebellum adapts feedforward movement control. Current opinion in neurobiology Available at: http://www.sciencedirect.com/science/article/pii/S0959438806001395.

Binkofski F, Buxbaum LJ (2013) Two action systems in the human brain. Brain Lang 127:222–229.

Boe S, Gionfriddo A, Kraeutner S, Tremblay A, Little G, Bardouille T (2014) Laterality of brain activity during motor imagery is modulated by the provision of source level neurofeedback. Neuroimage 101:159–167.

Brooks JX, Cullen KE (2013) The Primate Cerebellum Selectively Encodes Unexpected Self-Motion. Curr Biol 23:947–955.

Burianová H, Marstaller L, Sowman P, Tesan G, Rich A, Williams M, Savage G, Johnson B (2013) Multimodal functional imaging of motor imagery using a novel paradigm. NeuroImage 71:50–58.

Censor N, Dayan E, Cohen LG (2014) Cortico-subcortical neuronal circuitry associated with reconsolidation of human procedural memories. Cortex; a journal devoted to the study of the nervous system and behavior 58:281–288.

Chang Y, Lee J-J, Seo J-H, Song H-J, Kim Y-T, Lee H, Kim H, Lee J, Kim W, Woo M, Kim J (2010) Neural correlates of motor imagery for elite archers. NMR in Biomedicine 24:366-72.

Culham J, Cavina-Pratesi C, Singhal A (2006) The role of parietal cortex in visuomotor control: What have we learned from neuroimaging? Neuropsychologia 44:2668–2684.

Cumming J, Eaves DL (2018) The Nature, Measurement, and Development of Imagery Ability. Imagination, Cognition and Personality 37:375–393.

Cunnington R, Windischberger C, Moser E (2005) Premovement activity of the pre-supplementary motor area and the readiness for action: Studies of time-resolved event-related functional MRI. Human Movement Science 24:644–656.

Dayan E, Cohen LG (2011) Neuroplasticity subserving motor skill learning. Neuron 72:443–454.

Debarnot U, Sperduti M, Di Rienzo F, Guillot A (2014) Experts bodies, experts minds: How physical and mental training shape the brain. Front Hum Neurosci 8:280.

Di Rienzo F, Debarnot U, Daligault S, Saruco E, Delpuech C, Doyon J, Collet C, Guillot A (2016) Online and Offline Performance Gains Following Motor Imagery Practice: A Comprehensive Review of Behavioral and Neuroimaging Studies. Front Hum Neurosci 10:315.

Didier JJ, Li L, Magill RA (2013) Environmental context affects outcome and kinematic changes at different rates during skill learning. Percept Mot Skills 116:953–968.

Doyon J, Benali H (2005) Reorganization and plasticity in the adult brain during learning of motor skills. Curr Opin Neurobiol 15:161–167.

Driskell J, Copper C, Moran A (1994) Does mental practice enhance performance? Journal of Applied Psychology 79:481.

Duann J-RR, Chiou J-CC (2016) A Comparison of Independent Event-Related Desynchronization Responses in Motor-Related Brain Areas to Movement Execution, Movement Imagery, and Movement Observation. PLoS ONE 11:e0162546.

Eaves DL, Emerson JR, Binks JA, Scott MW, Kenny RPWP (2018) Imagery ability: the individual difference gradient and novel training methods (Commentary on Kraeutner et al. (2018)). Eur J Neurosci 47:1219–1220.

Edwards B, Lindsay K, Waterhouse J (2005) Effect of time of day on the accuracy and consistency of the badminton serve. Ergonomics 48:1488–1498.

Edwards B, Waterhouse J, Atkinson G, Reilly T, Edwards B, Waterhouse J, Atkinson G, Reilly T (2007) Effects of time of day and distance upon accuracy and consistency of throwing darts. Journal of Sports Sciences 25:1531–1538.

Elliott R, Dolan RJ, Frith CD (2000) Dissociable functions in the medial and lateral orbitofrontal cortex: evidence from human neuroimaging studies. Cereb Cortex 10:308–317.

Evans C, Edwards MG, Taylor LJ, Ietswaart M (2016) Perceptual decisions regarding object manipulation are selectively impaired in apraxia or when tDCS is applied over the left IPL. Neuropsychologia 86:153–166.

Flash T, Bizzi E (2016) Cortical circuits and modules in movement generation: experiments and theories. Curr Opin Neurobiol 41:174–178.

Frank C, Land WM, Popp C, Schack T (2014) Mental representation and mental practice: experimental investigation on the functional links between motor memory and motor imagery. PLoS ONE 9:e95175.

Frank C, Land WM, Schack T (2015) Perceptual-Cognitive Changes During Motor Learning: The Influence of Mental and Physical Practice on Mental Representation, Gaze Behavior, and Performance of a Complex Action. Front Psychol 6:1981.

Frank C, Schack T (2017) The Representation of Motor (Inter)action, States of Action, and Learning: Three Perspectives on Motor Learning by Way of Imagery and Execution. Front Psychol 8:678.

Gentili R, Han CE, Schweighofer N, Papaxanthis C (2010) Motor learning without doing: trial-by-trial improvement in motor performance during mental training. J Neurophysiol 104:774–783.

Gentili R, Papaxanthis C, Pozzo T (2006) Improvement and generalization of arm motor performance through motor imagery practice. Neuroscience 137:761–772.

Gregg M, Hall C, Butler A (2010) The MIQ-RS: A Suitable Option for Examining Movement Imagery Ability. Evid Based Complement Alternat Med 7:249–257.

Gregg M, Hall C, Nederhof E (2005) The imagery ability, imagery use, and performance relationship. The Sport Psychologist 19:93–99.

Hanakawa T, Dimyan M, Hallett M (2008) Motor Planning, Imagery, and Execution in the Distributed Motor Network: A Time-Course Study with Functional MRI. Cerebral Cortex 18:2775–2788.

Hancock GR, Butler MS, Fischman MG (1995) On the Problem of Two-Dimensional Error Scores: Measures and Analyses of Accuracy, Bias, and Consistency. J Mot Behav 27:241–250.

Hansen C, Rezzoug N, Gorce P, Isableu B (2012) Is the time of release during a precision throwing task, predictable? Comput Method Biomec 15:250–252.

Hardwick R, Rottschy C, Miall R, Eickhoff S (2013) A quantitative meta-analysis and review of motor learning in the human brain. NeuroImage 67:283–297.

Hardwick RM, Caspers S, Eickhoff SB, Swinnen SP (2018) Neural correlates of action: Comparing meta-analyses of imagery, observation, and execution. Neurosci Biobehav Rev 94:31–44.

Hétu S, Grégoire M, Saimpont A, Coll M-P, Eugène F, Michon P-E, Jackson P (2013) The neural network of motor imagery: An ALE meta-analysis. Neuroscience and biobehavioral reviews 37:930–949.

Ingram TG, Kraeutner SN, Solomon JP, Westwood DA, Boe SG (2016) Skill acquisition via motor imagery relies on both motor and perceptual learning. Behav Neurosci 130:252–260.

Ingram TG, Solomon JP, Westwood DA, Boe SG (2019) Movement related sensory feedback is not necessary for learning to execute a motor skill. Behav Brain Res 359:135–142.

Jackson P, Lafleur M, Malouin F, Richards C, Doyon J (2003) Functional cerebral reorganization following motor sequence learning through mental practice with motor imagery. NeuroImage 20:1171–1180.

Jenkinson M, Bannister P, Brady M, Smith S (2002) Improved optimization for the robust and accurate linear registration and motion correction of brain images. Neuroimage 17:825–41.

Kilteni K, Andersson BJ, Houborg C, Ehrsson HH (2018) Motor imagery involves predicting the sensory consequences of the imagined movement. Nat Commun 9:187.

Kraeutner S, Gionfriddo A, Bardouille T, Boe S (2014) Motor imagery-based brain activity parallels that of motor execution: Evidence from magnetic source imaging of cortical oscillations. Brain research 1588:81–91.

Kraeutner SN, El-Serafi M, Lee J, Boe SG (2019) Disruption of motor imagery performance following inhibition of the left inferior parietal lobe. Neuropsychologia 127:106-112.

Kraeutner SN, Ingram TGJG, Boe SG (2017) The effector independent nature of motor imagery: Evidence from rTMS induced inhibition to the primary motor cortices. Neuropsychologia 97:1–8.

Kraeutner SN, Keeler LT, Boe SG (2016a) Motor imagery-based skill acquisition disrupted following rTMS of the inferior parietal lobule. Experimental brain research 234:397–407.

Kraeutner SN, MacKenzie LA, Westwood DA, Boe SG (2016b) Characterizing skill acquisition through motor imagery with no prior physical practice. Journal of experimental psychology Human perception and performance 42:257–265.

Kraeutner SN, McWhinney SR, Solomon JP, Dithurbide L, Boe SG (2018) Experience modulates motor imagery-based brain activity. Eur J Neurosci 47:1221–1229.

Kremer P, Spittle M, McNeil D, Shinners C (2009) Amount of mental practice and performance of a simple motor task. Percept Mot Skills 109:347–356.

Kumar A, Tanaka Y, Grigoriadis A, Grigoriadis J, Trulsson M, Svensson P (2017) Training-induced dynamics of accuracy and precision in human motor control. Sci Rep-uk 7:6784.

Lacourse MG, Orr EL, Cramer SC, Cohen MJ (2005) Brain activation during execution and motor imagery of novel and skilled sequential hand movements. Neuroimage 27:505–519.

Lacourse MG, Turner JA, Randolph-Orr E, Schandler SL, Cohen MJ (2004) Cerebral and cerebellar sensorimotor plasticity following motor imagery-based mental practice of a sequential movement. J Rehabil Res Dev 41:505–524.

Land WM, Liu B, Cordova A, Fang M, Huang Y, Yao WX (2016) Effects of Physical Practice and Imagery Practice on Bilateral Transfer in Learning a Sequential Tapping Task. PLoS ONE 11:e0152228.

Lebon F, Lotze M, Stinear C, Byblow W (2012) Task-Dependent Interaction between Parietal and Contralateral Primary Motor Cortex during Explicit versus Implicit Motor Imagery. PLoS ONE 7:e37850.

Li C-S, Padoa-Schioppa C, Bizzi E (2001) Neuronal Correlates of Motor Performance and Motor Learning in the Primary Motor Cortex of Monkeys Adapting to an External Force Field. Neuron 30:593–607.

Lohse K, Healy A, Sherwood D (2010a) Mental Practice in the Intermanual Transfer of Motor Skills. J Imag Res Sport Phys Activity 5.

Lohse KR, Sherwood DE, Healy AF (2010b) How changing the focus of attention affects performance, kinematics, and electromyography in dart throwing. Hum Mov Sci 29:542–555.

McDonald PV, van Emmerik RE, Newell KM (1989) The effects of practice on limb kinematics in a throwing task. J Mot Behav 21:245–264.

Mendoza D, Wichman H (1978) “Inner” darts: effects of mental practice on performance of dart throwing. Percept Mot Skills 47:1195–1199.

Miall RC, Wolpert DM (1996) Forward Models for Physiological Motor Control. Neural Networks 9:1265–1279.

Milton J, Solodkin A, Hluatík P, Small S (2007) The mind of expert motor performance is cool and focused. NeuroImage 35:804–813.

Mizuguchi N, Nakata H, Kanosue K (2014) Effector-independent brain activity during motor imagery of the upper and lower limbs: an fMRI study. Neurosci Lett 581:69–74.

Nachev P, Kennard C, Husain M (2008) Functional role of the supplementary and pre-supplementary motor areas. Nature Reviews Neuroscience 9:nrn2478.

Nakata H, Yoshie M, Miura A, Kudo K (2010) Characteristics of the athletes' brain: evidence from neurophysiology and neuroimaging. Brain Res Rev 62:197–211.

O'Shea H, Moran A (2017) Does Motor Simulation Theory Explain the Cognitive Mechanisms Underlying Motor Imagery? A Critical Review. Front Hum Neurosci 11:72.

Oldfield RC (1971) The assessment and analysis of handedness: The Edinburgh inventory. Neuropsychologia 9:97113.

Olsson C -J., Nyberg (2010) Motor imagery: if you can't do it, you won't think it. Scand J Med Sci Spor 20:711–715.

Olsson C-J, Jonsson B, Nyberg L (2008a) Learning by doing and learning by thinking: an fMRI study of combining motor and mental training. Frontiers in Human Neuroscience 2:5.

Olsson C-JJ, Jonsson B, Larsson A, Nyberg L (2008b) Motor representations and practice affect brain systems underlying imagery: an FMRI study of internal imagery in novices and active high jumpers. Open Neuroimag J 2:5–13.

Padoa-Schioppa C, Li C-S, Bizzi E (2002) Neuronal Correlates of Kinematics-to-Dynamics Transformation in the Supplementary Motor Area. Neuron 36:751–765.

Padoa-Schioppa C, Li C-SRS, Bizzi E (2004) Neuronal activity in the supplementary motor area of monkeys adapting to a new dynamic environment. J Neurophysiol 91:449–473.

Penhune VB, Doyon J (2002) Dynamic cortical and subcortical networks in learning and delayed recall of timed motor sequences. J Neurosci 22:1397–1406.

Pfurtscheller G, Neuper C (1997) Motor imagery activates primary sensorimotor area in humans. Neuroscience Letters 239:6568.

Popa LS, Hewitt AL, Ebner TJ (2012) Predictive and feedback performance errors are signaled in the simple spike discharge of individual Purkinje cells. J Neurosci 32:15345–15358.

Querfurth S, Schücker L, de Lussanet M, Zentgraf K (2016) An Internal Focus Leads to Longer Quiet Eye Durations in Novice Dart Players. Frontiers Psychology 7:633.

Rizzolatti G, Cattaneo L, Fabbri-Destro M, Rozzi S (2014) Cortical mechanisms underlying the organization of goal-directed actions and mirror neuron-based action understanding. Physiol Rev 94:655–706.

Rizzolatti G, Luppino G, Matelli M (1998) The organization of the cortical motor system: new concepts. Electroen Clin Neuro 106:283–296.

Rizzolatti G, Matelli M (2003) Two different streams form the dorsal visual system: anatomy and functions. Experimental Brain Research 153:146–157.

Roland PE, Larsen B, Lassen NA, Skinhøj E (1980) Supplementary motor area and other cortical areas in organization of voluntary movements in man. J Neurophysiol 43:118–136.

Ruffino C, Papaxanthis C, Lebon F (2017) Neural plasticity during motor learning with motor imagery practice: Review and perspectives. Neuroscience 341:61–78.

Schorer J, Jaitner T, Wollny R, Fath F, Baker J (2012) Influence of varying focus of attention conditions on dart throwing performance in experts and novices. Exp Brain Res 217:287–297.

Schuster C, Hilfiker R, Amft O, Scheidhauer A, Andrews B, Butler J, Kischka U, Ettlin T (2011) Best practice for motor imagery: a systematic literature review on motor imagery training elements in five different disciplines. BMC medicine 9:75.

Seitz RJ, Canavan AG, Yágüez L, Herzog H, Teilmann L, Knorr U, Huang Y, Hömberg V (1994) Successive roles of the cerebellum and premotor cortices in trajectorial learning. Neuroreport: An International Journal for the Rapid Communication of Research in Neuroscience.

Sherwood DE, Lohse KR, Healy AF (2014) Judging joint angles and movement outcome: Shifting the focus of attention in dart-throwing. J Exp Psychol Hum Percept Perform 40:1903–1914.

Smeets JB, Frens MA, Brenner E (2002) Throwing darts: timing is not the limiting factor. Experimental Brain Research 144:268–274.

Smith S (2002) Fast robust automated brain extraction. Human Brain Mapping 17:143–155.

Smith SM, Jenkinson M, Woolrich MW et al (2004) Advances in functional and structural MR image analysis and implementation as FSL. Neuroimage 23(Suppl 1):S208–S219.

Solodkin A (2004) Fine Modulation in Network Activation during Motor Execution and Motor Imagery. Cerebral Cortex 14:1246–1255.

Spittle M, Kremer P (2010) Mental practice and the retention of motor learning: a pilot study. Percept Mot Skills 110:888–896.

Stinear C, Byblow W, Steyvers M, Levin O, Swinnen S (2006) Kinesthetic, but not visual, motor imagery modulates corticomotor excitability. Experimental Brain Research 168:157–164.

Sutton B, Ouyang C, Karampinos D, Miller G (2009) Current trends and challenges in MRI acquisitions to investigate brain function. International Journal of Psychophysiology 73:33–42.

Tanji J, Kurata K (1982) Comparison of movement-related activity in two cortical motor areas of primates. J Neurophysiol 48:633–653.

Tanji J, Shima K (1996) Supplementary motor cortex in organization of movement. Eur Neurol 36 Suppl 1:13–19.

Tyč F, Boyadjian A (2011) Plasticity of motor cortex induced by coordination and training. Clin Neurophysiol 122:153–162.

Ungerleider LG, Doyon J, Karni A (2002) Imaging brain plasticity during motor skill learning. Neurobiol Learn Mem 78:553–564.

Wei G, Luo J (2010) Sport expert’s motor imagery: functional imaging of professional motor skills and simple motor skills. Brain Res 1341:52–62.

Wohldmann EL, Healy AF, Lyle BEJ (2007) Pushing the limits of imagination: Mental practice for learning sequences. Journal of Experimental Psychology: Learning, Memory, and Cognition 33:254261.

Wolpert DM, Miall RC, Kawato M (1998) Internal models in the cerebellum. Trends Cogn Sci (Regul Ed) 2:338–347.

World Darts Federation (2017): WDF Playing and Tournament Rules July 25, 2017. Available from: URL: http://www.dartswdf.com/rules/.

Yarrow K, Brown P, Krakauer JW (2009) Inside the brain of an elite athlete: the neural processes that support high achievement in sports. Nat Rev Neurosci 10:585–596.

Zhang H, Xu L, Wang S, Xie B, Guo J, Long Z, Yao L (2011) Behavioral improvements and brain functional alterations by motor imagery training. Brain research 1407:38–46.

Chapter 4 : NEURAL AND BEHAVIOURAL EVIDENCE FOR MOTOR IMAGERY AS SCAFFOLDING FOR SKILL ACQUISITION

4.0 ABSTRACT

While considered analogous to physical practice (PP), the nature of motor imagery-based skill acquisition is not well understood. Whether or not motor imagery (MI) can facilitate both alterations to motor representations, and mapping of these representations to specific effectors has not been probed. Here, we examined the nature of skill acquisition via motor imagery by examining the effect of motor imagery-based training applied either prior to, or after physical practice-based training. Participants (*N* = 38) engaged in ten days of training of a dart throwing task, involving either five days of MI prior to PP (MI-PP), or MI following PP (PP-MI), or only PP (PP-only). Performance-related outcomes were assessed throughout. Brain activity (functional magnetic resonance imaging; fMRI) was also obtained at three time points (pre/mid/post-training) for the MI-PP and PP-MI groups. Behavioural results are two-fold: MI-based practice led to robust changes in global vs. specific aspects of the movement, but only when applied in the first half of training. Further, overall (after day ten), performance was greater when MI preceded PP, yet applying imagery remained inferior to changes driven solely via PP. Between-group analyses of fMRI data at mid-training revealed greater activation for the PP-MI group (PP-MI > MI-PP), localized to regions that support effector dependent encoding, yet no between-group differences in brain activation were observed post-training. Findings indicate that MI drives changes in global aspects of a movement, reflecting effector independent encoding central

to early stages of skill acquisition. Ultimately, this work provides new information related to the mechanism of how skill acquisition occurs via MI.

4.1 INTRODUCTION

A glaring difference between motor imagery (MI) and physical practice (PP) is the absence of feedback about task performance given the lack of overt execution in MI. Notwithstanding this difference, MI has long been considered analogous to PP, sharing neural representations to simulate movement without overt execution (Jeannerod, 2001; Moran et al., 2012; Wakefield et al., 2013). These shared neural representations, or ‘functional equivalence’, are thought to provide the basis for its effectiveness in driving skill acquisition in the absence of over movement (Jeannerod, 2001; Moran et al., 2012; Wakefield et al., 2013). Contesting this long-standing assumption, recent work has theorized that MI facilitates skill acquisition differently than PP: only global or abstract encoding is driven as opposed to effector specific encoding, leading to less robust alterations to the motor program and in turn marginal improvements in performance (Frank and Schack, 2017; Ingram et al., 2019; Ingram et al., 2016; Kraeutner et al., 2017; Land et al., 2016). In the context of Fitts and Posner’s framework (1967), in which skill acquisition occurs over the cognitive, associative, and autonomous stages, the notion that MI drives global or abstract encoding suggests that motor imagery lends itself to facilitating the cognitive stage of skill acquisition. Thus, it may be most useful in creating scaffolding during the early stages of learning for which improvements in performance can then be more readily facilitated through physical practice in the later stages. Yet, our knowledge of the nature of MI-based skill acquisition remains severely incomplete, and this notion has not been probed in the motor imagery literature.

Proficiency on a given motor task is achieved through both effector independent (i.e., encoding of abstract or global movement features, related to integrating perceptual information to movement goals that is not specific to an effector group) and dependent (i.e., mapping the movement goals and specific movement parameters to the effector to be used in the task) encoding (Bapi et al., 2000; Cohen et al., 1990; Grafton et al., 1998; MacKay, 1982). Yet, owing to the covert nature of MI, whether or not the motor program is mapped to a specific effector is unknown. Converging evidence suggests that the motor program is not mapped to a specific effector in MI; rather, that MI facilitates effector independent encoding (Land et al., 2016; Ingram et al., 2016; Kraeutner et al., 2017; Kraeutner, Keeler, et al., 2016; Lohse et al., 2010a; Mizuguchi et al., 2014), and that skill proficiency cannot be facilitated through MI alone. Behaviourally, work employing transfer tasks show that MI-based training leads to similar improvements in performance in both trained and untrained effectors (Land et al., 2016), and greater perceptual encoding is facilitated through MI-based training (Ingram et al., 2016). Further, the absence of effector dependent encoding achieved through MI is supported as inhibition to primary motor cortex, a brain region that supports this form of encoding, does not impact MI-based learning (Kraeutner et al., 2017) and activation localized to this region is inconsistently reported in the MI neuroimaging literature (Grèzes and Decety, 2001; Hardwick et al., 2018; Hétu et al., 2013).

Although mounting evidence suggests that MI relies on effector independent encoding, probing the nature of MI-based skill acquisition through the manipulation of practice modality has not been done. That MI encodes effector independent representations suggests it is most effective in the early stages of learning as scaffolding for which effector dependent encoding can be more readily facilitated through PP for greater improvements in performance. In contrast however, this scaffolding or development of the effector independent representation of the skill would be rendered ineffective later in the stages of learning once alterations to the motor program have occurred. Here, we designed an experiment to test the theory that MI facilitates effector independent encoding, yet that skill proficiency cannot be facilitated through MI alone. We employed a crossover design whereby participants trained on a complex motor skill, dart throwing, via PP followed by MI (PP-MI), or via MI followed by PP (MI-PP). We hypothesized that, given an equal dose of MI and PP, the greatest gains in task performance should be observed when PP-based training is *preceded* by MI-based training. We argue that, based on the above theoretical framework, improvements in performance that result from five days of PP would not be equivalent between groups, and would instead depend on when MI was applied in the training timeline.

To address our prediction, we assessed training-related changes in performance through physical testing sessions in a pre/post design for each practice modality (Fig. 4.1). Performance was measured in terms of in task-related outcomes, including spatial accuracy, consistency, and trial-by-trial corrections, and kinematics (i.e., joint angles and timing parameters). Brain activity during MI of the trained task was also examined, with participants undergoing functional magnetic resonance imaging (fMRI) at three time points (pre/mid/post training). Between- and within-group analyses were performed to characterise functional brain changes during MI of the task as a function of training modality and order over the course of training. A third group of participants did not undergo fMRI but engaged in ten days of PP-based training, which allowed us to anchor our findings to the ‘gold standard’ of practice.

4.2 METHODS

4.2.1 Participants

Thirty-eight participants (right handed, as determined by a score of ≥40 on the Edinburgh Handedness Inventory [Oldfield, 1971]) were recruited from the local and university community. The Nova Scotia Health Authority research ethics board approved the study. All participants were healthy, reported normal hearing, were free of neurological disorders, had no contraindications to MRI, and each provided written informed consent. All participants underwent 10 total practice sessions of a dart-throwing task, according to group assignment: motor imagery prior to PP ("MI-PP", motor imagery following PP ("PP-MI"), or PP for all sessions ("PP-only"). As this experiment is an extension of work reported in Chapter 3, participants in the MI-PP and PP-MI groups stemmed from the "MI" and "PP" groups in the study reported in Chapter 3, respectively.

4.2.2 Experimental Design

Training and testing sessions followed procedures as described in Chapter 3 (Fig. 4.1). Briefly, each training session lasted ~20 minutes and involved 15 blocks of dart throws, with six trials (dart throws) per block. Dart throwing was performed in accordance with World Dart Federation regulations (World Darts Federation, 2017), and participants were instructed to aim at the bullseye and to limit their throws to flexion and extension movements at the elbow in the sagittal plane. At the outset of training, all participants underwent a brief familiarization phase, involving a five minute video that provided exemplar performances, both male and female from both the 3rd and first person perspective. Participants performed darts throws using nickel/brass tipped darts that weighed 22g (PP sessions), or imagined performing throws cued by an auditory script delivered via noise-cancelling headphones (MI sessions). At the outset of each MI session, participants were first oriented to and instructed to perform kinaesthetic MI (i.e., 1st person perspective with an emphasis on the polysensory aspect of the task; (Schuster et al., 2011; Stinear et al., 2006). Physical test blocks comprised 18 total dart throws, performed in three blocks of six throws, lasting ~15 min, embedded at four points throughout training on days 1, 5, 6, and 10; Fig. 4.1 (similar to parameters employed in Lohse et al., 2010b; Tyč and Boyadjian, 2011; Querfurth et al., 2016; Fig. 4.1). The final location of each dart was digitized (Polhemus Fastrak, Colchester, VT) and video data were recorded to capture participant kinematics in the sagittal plane (Canon Powershot SX280 HS mounted perpendicular to the throwing line; Canon Canada, Inc.), and stored for offline analysis. Training sessions within either half of the study (days 1-5 or days 6-10) were required to be scheduled within ten days (i.e., averaging no more than 2 days apart) and the 'break' between testing sessions on day 5 and day 6, for which participants in the MI-PP and PP-MI groups underwent an fMRI session, was required to be no more than three days apart.

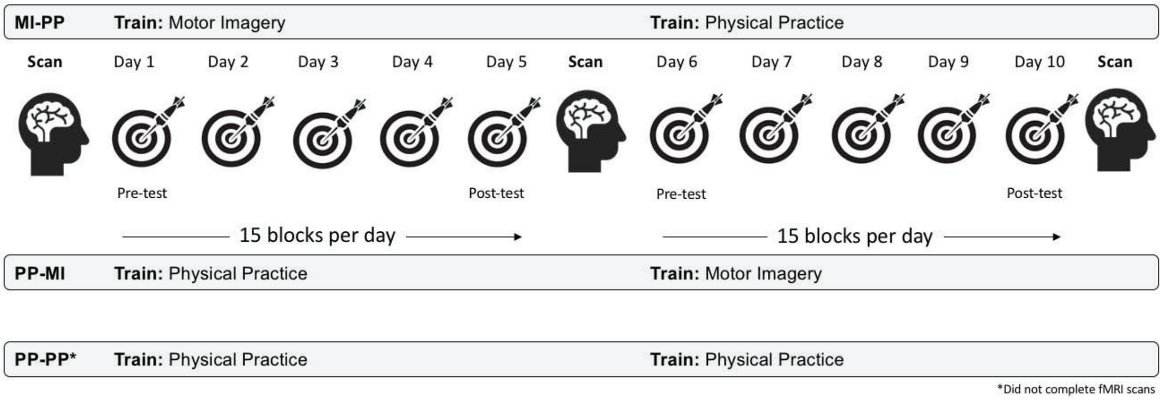


Figure 4.1 Timeline of the experimental design. Participants engaged in ten training sessions of a dart throwing task, via motor imagery prior to physical practice, motor imagery following physical practice, or physical practice only, based on group assignment. Participants completed four physical testing sessions in a pre/post design for each half of the study. Participants in the MI-PP and PP-MI groups also underwent three fMRI sessions (pre/mid/post-training) to capture changes in MI-related brain activation of the dart throwing task.

Structural and functional MRI data were acquired on a 3 Tesla GE MRI (GE Medical Systems, Waukesha, WI, with a 32 channel RF Head Coil). A 3D T1-weighted anatomical image was acquired using a IR-prepped fast spoiled gradient recalled echo (IR-FSPGR) sequence (inversion time (TI) = 450 ms, repetition time (TR) = 4.0ms, echo time (TE) = 1.33ms, flip angle = 9°, field of view (FOV) 25.6 cm, 256 × 256, 184 sagittal slices at 1 mm thickness, auto-calibrating reconstruction for cartesian imaging (ARC) phase acceleration = 1, ARC slice acceleration = 1). A T2-weighted anatomical image was acquired using a 3D CUBE sequence (inversion time (TI) = 400 ms, TR = 4200ms, TE = 101 ms, 140 Echo Train Length, 25.6cm FOV, 256 × 256, 184 sagittal slices at 1 mm thickness, ARC phase acceleration = 1.5, ARC slice acceleration = 1). Functional MRI data were acquired using a 2D multi-band echo-planar image (EPI) sequence (TR = 950ms, TE = 30 ms, flip angle = 60°, 21.6 cm FOV, 72 × 72, 3 mm thick slices, 224 volumes, MUX acceleration factor 3 slice direction, ARC acceleration factor 2 in-plane; Stanford Center for Cognitive and Neurobiological Imaging, http://cni.stanford.edu). Additional EPI reference scans with matching parameters except phase-encode blip direction reversal were acquired to facilitate field distortion correction (Andersson et al., 2003; Smith et al., 2004).

The fMRI experiment included four runs, each consisting of two MI blocks (28.5 sec) with alternating rest blocks (19 sec; eyes open). Each run began and ended with a rest block. The start of each MI block was cued visually. Participants were asked to visualize throwing six darts (equivalent to one training block) using kinaesthetic imagery with their eyes closed. Participants were cued to the completion of the imagery block via an auditory tone. Manipulation checks were administered after each run inquiring about the participants' level of engagement and the quality of imagery on a scale of 1 (not engaged; poor quality) to 5 (extremely engaged; excellent quality). Stimuli were presented using Presentation software (Neurobehavioral Systems, Inc. Berkley, CA) synchronized to MRI data acquisition, on a mylar screen positioned across the scanner bore via an LCD projector. Participants viewed the stimuli via an angled mirror. Prior to the fMRI experiment, participants completed a self-report MI questionnaire (Motor Imagery Questionnaire-Revised Second Version; MIQ-RS; Gregg et al., 2005, 2010; Butler et al., 2012) to ensure there were no pre-existing group differences in imagery, and engaged in a familiarization period whereby participants were oriented to the task and type of MI (first person, kinaesthetic) whereby they listened to an auditory script and watched a 30 sec clip of the darts task. Participants in the PP-MI and MI-PP groups underwent fMRI sessions at three time points (pre/mid/post).

4.2.3 Behavioural analysis

All statistical analyses were performed using R (R project for statistical computing) with an a priori alpha of 0.05 denoting significance. For the participants in the MI-PP and PP-MI groups, separate ANOVAs were conducted to ensure similarity in imagery performance and ability across groups. Specifically, MIQ-RS scores were tabulated across participants for each imagery condition (kinaesthetic and visual) and a 2 (imagery condition) X 2 (group) mixed ANOVA was conducted to assess the between group effects of imagery condition on MIQ-RS score, as previously reported in Chapter 3. Responses for both manipulation checks during the neuroimaging sessions were averaged across participants for each run and scan to ensure similarity in imagery performance across groups. Separate 3 (time point) X 2 (group) mixed ANOVAs were conducted on each outcome measure (engagement, quality) to assess the between group effects on task engagement and imagery quality.

For all performance related outcomes, following prior work, the first throw of each test block was considered a 'warmup' and excluded from statistical analyses. (i.e., leaving 15 total throws per test session). Outliers were identified as throws that exceeded three standard deviations above the mean for each participant across sessions and were removed from further analyses. Our task-related outcomes, radial error (RE) was calculated for each throw, and consistency (bivariate variable error; BVE; Hancock et al., 1995; Edwards et al., 2007; Lohse et al., 2010b; Schorer et al., 2012; Sherwood et al., 2014; Querfurth et al., 2016) were derived from the digitized data (with the bullseye considered the point of origin (0,0) and error calculated in the X and Y plane from the point of origin). Notably, as RE does not capture directional information related to performance, we did not provide this information as a form of feedback to our participants (i.e., in addition to the visual feedback of their performance they received after each physical dart throw). Changes related to RE were assessed using a linear mixed effects (LME) model conducted using the LME4 package (Bates et al., 2015) in assessing RE on the darts throwing task as a function of group, time point, and their interaction with participant entered as a random effect. A model including age and sex was shown to significantly improve the base model, measured using Akaike Information Criterion (Akaike, 1974). Thus, we included terms for age and sex in the final model. This same analysis could not be applied to BVE data, as BVE is calculated across throws within a session, thus BVE was determined for each participant at each test session, and separate Kruskal-Wallis rank sum tests were conducted to analyze the between-group effects at each time point (i.e., as data for BVE did not meet the assumptions of ANOVA). Mean RE was also determined for each participant at each test session, and effect sizes were calculated on both mean RE and BVE within each group (i.e., between test sessions) to characterise improvements in performance.

ACF1. The autocorrelation lag-1 (ACF1) is a coefficient of the correlation of two values in time series, and was employed to quantify the distance between two consecutive movements resulting in a measure of the correction factor of throws made on a trial-by-trial basis (Nelson-Wong et al., 2009; van Beers, 2009; van Beers et al., 2013). The ACF1 was calculated separately for deviations in the X and Y plane from the point of origin (0,0) using the digitized data, and with the mean correction factor calculated across the two planes. Specifically, AFC1 = 0 indicates that the relationship between endpoints of two consecutive movements is random; thus, a mean of zero reflects novice performance. Yet, as ACF1 approaches 1, error between endpoints of two consecutive movements decreases (i.e., improvement occurs between throws), thus reflecting skill acquisition. Therefore, learning is indicated as the ACF1 approaches 1. Formally, the ACF1 in the X and Y planes are defined as follows:

$$ACF1_x = \frac{E\{x(n)x(n+1)\}}{E\{x(n)x(n)\}}$$

$$ACF1_y = \frac{E\{y(n)y(n+1)\}}{E\{y(n)y(n)\}}$$

The ACF1 analysis was applied using customized functions in MATLAB (Mathworks, Inc). The full proof of the ACF1 calculation is available as Supplementary Materials (see Appendix B).

Following prior work, initial kinematic variables of interest included shoulder angle, elbow angle, release and preparation time (Lohse et al., 2010; Sherwood et al., 2014), and were derived from video data, analyzed using Dartfish Pro motion analysis software (Dartfish HQ, Fribourg, Switzerland). Joint angles were assessed at two points of the dart throw (i.e., during 'take back' or maximum flexion of the elbow, and during the 'release point' or the point at which the dart left the participant's hand), by placing anatomical markers placed on the acromion process, olecranon, and highest point of the iliac crest in line with the coronal plane of the body (for shoulder angle) or styloid process of the throwing arm (for elbow angle). Release time was defined as the time between maximum elbow flexion to the point of release. Preparation time was defined as the time between the point of release to maximum flexion of the subsequent throw. Yet, as little is known about the best kinematics to predict performance on a darts throwing task amongst non-experts, we conducted an exploratory analysis to identify which variables best predicted performance. In particular, a linear mixed model was conducted using the LME4 package (Bates et al., 2015) assessing MRE on the darts throwing task as a function of the aforementioned kinematic outcomes (shoulder and elbow angles at maximum flexion and release, preparation and release time) entered as fixed effects, and participant entered as a random effect (Table 4.4). Shoulder and elbow angles at release in conjunction with shoulder angle at take back were determined to predict accuracy of the darts throw (Table 4.4). Next, we computed a ‘global kinematic variability’ score, equally weighted across these three variables (using SD calculated across trials per test session) for each participant; Lohse et al., 2010), for group-level analyses. We also calculated angular velocity, defined as the elbow angle at maximum flexion subtracted from the point of release and divided by the throwing time, to assess changes in average angular velocity as a function of training at the group-level (Lohse et al., 2010). Separate 3 (group) X 4 (time point) mixed ANOVAs were conducted on global kinematic variability and angular velocity to assess the between-group effects of training, and effect sizes were calculated to characterise training-related improvements in performance for both halves of training, as well as overall (i.e, between day 1 and 5, day 6 and 10, and day 1 and 10, respectively).

4.2.4 fMRI preprocessing and analysis

All f/MRI data was processed using the Oxford Centre for Functional MRI of the Brain’s (FMRIB) software library (FSL v.5.0.10; FMRIB Oxford, www.fmrib.ox.ac.uk/fsl) and fMRI Expert Analysis Tool (FEAT) version 5.0.10 [Smith et al., 2004; part of FSL). Anatomical data (T1 and T2 scans) was preprocessed using FLIRT and FNIRT to perform registration-based skull-stripping to template brain MNI152_T1_1mm. Functional data was preprocessed (including motion correction with MCFLIRT (Jenkinson et al., 2002), field inhomogeneity-induced distortion correction with reverse-phase encoded blips using TOPUP (Andersson et al., 2003), brain extraction using BET (Smith et al., 2002), spatial smoothing using a Gaussian kernel (FWHM 5mm), and high-pass temporal filtering at 0.01 Hz to remove low-frequency noise) and images were then rigid-body spatially co-registered (using 6DOF) to the processed anatomical image using FLIRT. Further, images were then combined with the non-linear registration to MNI152_1mm with a voxel size of 3mm for group comparison of individual fMRI results.

Individual statistical activation maps were calculated within each run using a general linear model (GLM) with FEAT, with motion outliers included as confounds, determined from a contrast of imagery (darts) vs. rest computed for each run (first-level analysis). A second-level analysis combined all runs in a fixed effects model to produce contrast of parameter estimate (COPE) maps for each individual and time point (pre/mid/post). High-level group analyses were carried out using FLAME (FMRIB's Local Analysis of Mixed Effects) model with FEAT using the averages of the lower-level COPE maps, to assess the impact of training modality on resultant patterns of MI-related brain activity. Specifically, between-group comparisons were conducted at each time point (i.e., pre/mid/post-training). Consistency (BVE) was added as a covariate for the comparisons at the mid- and post-training scan. Within-group comparisons for the first and second half of training (i.e., pre- vs. mid-training scan; and mid- vs. post-training scan) were conducted for each group. Of note, between- and within-group comparisons for the pre and mid-training scan are previously reported in Chapter 3. All analyses used a corrected cluster threshold of $Z > 2.0$ and significance threshold of $p < .05$, corrected for family-wise error.

4.3 RESULTS

Three participants were excluded from the study (one from the MI-PP group because they dropped out during day 1; one from the PP-MI group for excess head motion during scanning), leaving 36 participants (MI-PP group: $n = 11$, 7 female; aged 24.5 ± 4.2 years; PP-MI group: $n = 11$, 8 female; aged 24.6 ± 4.7 years; PP-only group $n = 14$, 12 female; aged 23.2 ± 3.0 years). One participant from the PP-MI group only engaged in two of the three blocks during each testing session and had a four day break between day 5 and day 6 testing sessions due to technical issues related to the fMRI scanner. One additional participant from the PP-MI group had an incomplete data set in that the end location of each dart throw was not recorded for day 1, due to experimental error. No pre-existing group differences in motor imagery ability, were observed as determined via scores tabulated from the MIQ-RS (Gregg et al., 2005; Gregg et al., 2010), in that no effects of group ($F_{1,20} = 3.34$, $p = 0.08$), imagery condition ($F_{1,20} = 0.33$, $p = 0.57$), or interaction between group and imagery condition ($F_{1,20} = 0.33$, $p = 0.57$) were observed (Table 4.1). Further, no differences in task performance was observed throughout the experiment as determined via manipulation checks of imagery engagement [$F_{group}(1,20) = 0.44$, $p = 0.52$; $F_{time\ point}(2,40) = 0.39$, $p = 0.68$; $F_{interaction}(2,40) = 1.15$, $p = 0.33$] and imagery quality [$F_{group}(1,20) = 2.25$, $p = 0.15$; $F_{time\ point}(2,40) = 3.93$, $p = 0.32$; $F_{interaction}(2,40) = 3.93$, $p = 0.47$] conducted throughout the neuroimaging sessions (see Table 4.1).

Table 4.1

MIQ-RS scores and data from imagery manipulation checks conducted during neuroimaging sessions (mean and SD for each group). Data for the first half of the study is previously reported in Chapter 3).

		Group	
		MI-PP	PP-MI
MIQ-RS score	Kinaesthetic (/49)	35.6 (12.0)	38.7 (8.1)
	Visual (/49)	38.7 (8.3)	39.9 (7.3)
	Time point		
MI engagement (/5)	Pre-training	4.3 (0.7)	4.3 (0.5)
	Mid-training	4.3 (0.7)	4.1 (0.6)
	Post-training	4.4 (0.7)	4.1 (0.7)
MI quality (/5)	Pre-training	4.2 (0.7)	4.0 (0.7)
	Mid-training	4.3 (0.6)	3.9 (0.6)
	Post-training	4.4 (0.5)	4.0 (0.5)

Using standard analysis procedures for dart-throwing tasks, performance change was measured in terms of accuracy (RE) and consistency (BVE; see Table 4.2 for group means; Edwards et al., 2007; Hancock et al., 1995; Lohse et al., 2010b; Querfurth et al., 2016; Schorer et al., 2012; Sherwood et al., 2014). Table 4.3 shows results from linear mixed effects analysis conducted to assess RE as a function of group, time point, the interaction between group and time point, and participant entered as a random factor. Terms for age and sex were also included in the model (Table 4.3). Interactions between group and time point were significant (see Table 4.3) at days 5 and 6, but not at day 10, indicating that a bout of PP led to greater improvements in RE relative to an equivalent bout of MI, yet all groups reached a similar level of expertise after training. Change in RE within each group (i.e., between test sessions) was further characterized via effect sizes, with a large improvement in RE overall (day 10 minus day 1) observed for the PP-only and MI-PP groups, and a moderate improvement observed for the PP-MI group, indicating that MI was more effective when applied prior to PP (Table 4.2). Non-parametric analysis (see Methods) of BVE at each time point showed between-group differences at day 6 (i.e., retention; $H = 10.63$, $p = 0.005$) and trending at day 5 (i.e., acquisition; $H = 5.79$, $p = 0.055$). No differences were observed at day 1 (i.e., pre-training; $H = 0.90$, $p = 0.64$) or at day 10 (i.e., overall; $H = 0.66$, $p = 0.72$). As with RE, effect sizes calculated within each group (i.e., between test sessions) revealed a large improvement in BVE overall (i.e., day 1 vs. 10) for the PP-only and MI-PP group, and a moderate improvement for the PP-MI group (Table 4.2).

To add resolution to our performance analysis, we applied an ACF1 calculation to determine the correction factor between throws on a trial-by-trial basis (van Beers et al., 2013; van Beers, 2009; see Fig. 4.2 for a visualization). Specifically, through assessing the time point at which one gains the ability to correct between throws trial-trial would allow us to probe the onset of effector dependent encoding through an established forward model process. Interestingly, while a main effect of group on ACF1 was observed ($F_{2,131} = 3.21$, $p = 0.04$), no effect or time point, nor interaction between group and time point was observed ($F_{3,131} = 0.56$, $p = 0.65$; $F_{6,131} = 0.82$, $p = 0.56$, respectively). Yet, effect sizes calculated to characterise ACF1 changes driven via training separately for each group (see Table 4.2) revealed that meaningful changes in ACF1 were only observed in the second half of training regardless of order of modality (as evidenced via moderate effect sizes in the second half of training – day 6 vs. day 10 – in the MI-PP group and PP-MI groups). Overall (day 1 vs. day 10) however, the PP-only group demonstrated the greatest improvement in their ability to correct between throws on a trial-by-trial basis (evidenced via a large effect size; Table 4.3).

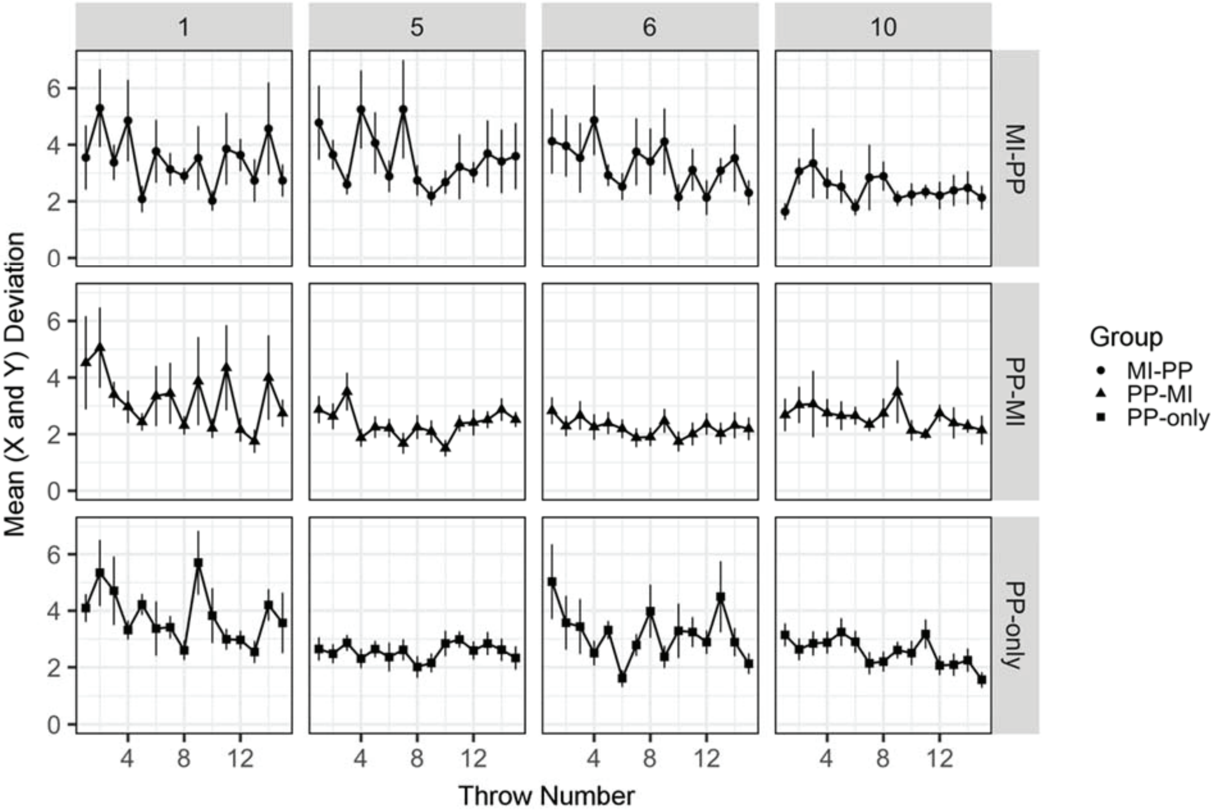


Figure 4.2 Visualization of trial-by-trial corrections. The average deviation from the bullseye in the X and Y plane are shown across throws for each testing session. As shown via autocorrelation lag-1 (ACF1) calculations and effect sizes within groups (Table 4.2), robust changes in ACF1 were observed in the second half of training (i.e., days 6 and 10).

Training-related changes in kinematics were assessed using motion capture analysis during the test sessions: 'global kinematic variability' (see Table 4.4) comprised shoulder angles at both the 'take back' and the point of release for each dart throw, as well as elbow angle at release; and angular velocity, defined as the change in elbow angle over throwing time. Only a significant main effect of time point was observed [F(3,96) = 11.31, $p < 0.001$], indicating that global kinematic variability decreased with training. No main effect of group nor interaction between group and time point was observed [F(2,32) = 0.65, $p = 0.53$; F(3,96) = 1.54, $p = 0.20$], correcting using Greenhouse-Geisser estimates of sphericity. Effect sizes calculated to characterise the change in kinematic outcomes across sessions show that global kinematic variability decreased via MI, regardless of when it was applied in training (Table 4.2). The changes driven via MI applied in training remained inferior to changes driven by PP-based training, as evidenced by a large effect size overall (day 1 vs. day 10) for the PP-group relative to moderate effect sizes observed in the PP-MI and MI-PP groups (Table 4.2). A similar trend was observed for angular velocity: we observed a significant main effect of time point [F(3,96) = 5.56, $p = 0.003$, yet no main effect of group [F(2,32) = 0.15, $p = 0.86$] nor significant interaction between group and time point [F(6,96) = 1.23, $p = 0.30$], corrected using Greenhouse-Geisser estimates of sphericity. Thus, angular velocity increased after training regardless of modality. Effect sizes showed that angular velocity also increased primarily in the early stages of training (Table 4.2).

Table 4.2

Behavioural data (mean and SD) for task-related performance outcomes (mean radial error; MRE, and bivariate variable error; BVE), and autocorrelation lag-1 (ACF1) calculation. Effect sizes conducted to characterise changes in performance (day 1 minus day 5; day 6 minus day 10; and day 1 minus day 10) are included. Improvements in performance are noted by negative effect sizes reflecting a decrease in error (MRE and BVE) and global kinematic variability, and positive effect sizes reflecting an increase in trial-by-trial correction factor (ACF) and angular velocity.

		Test session						
		Day 1	Day 5	d (1 vs. 5)	Day 6	Day 10	d (6 vs. 10)	d (1 vs. 10)
Mean Radial Error (cm)	MI-PP	8.70 (3.89)	8.93 (5.08)	0.05	8.37(5.41)	6.23(2.57)	-0.51	-0.75
	PP-MI	8.04 (4.05)	5.96 (1.41)	-0.69	5.75(1.27)	6.68(1.74)	0.61	-0.44
	PP-only	9.64(2.91)	6.42(1.36)	-1.42	8.04(1.61)	6.54(1.56)	-1.18	-1.33
Bivariate Variable Error (cm)	MI-PP	9.69 (4.72)	8.58 (3.84)	-0.26	8.30(3.33)	6.55(2.82)	-0.57	-0.81
	PP-MI	9.19 (4.92)	5.72 (1.24)	-0.97	5.97(1.15)	6.91(2.35)	0.51	-0.59
	PP-only	10.08 (3.98)	6.55(1.40)	-1.18	9.22 (2.94)	6.77 (1.61)	-1.04	-1.09
ACF1	MI-PP	0.19 (0.07)	0.14 (0.10)	-0.56	0.10 (0.08)	0.14 (0.10)	0.41	-0.56
	PP-MI	0.15 (0.13)	0.14 (0.12)	-0.07	0.14 (0.11)	0.18 (0.10)	0.39	0.28
	PP-only	0.16 (0.12)	0.19 (0.17)	0.16	0.22 (0.17)	0.24 (0.15)	0.14	0.58
Global Kinematic Variability	MI-PP	4.43 (2.1)	3.32 (1.3)	-0.52	4.43 (3.0)	3.19 (1.8)	-0.58	-0.58
	PP-MI	5.21 (2.3)	2.77 (2.0)	-1.36	3.23 (1.5)	2.78 (1.2)	-0.26	-1.36

	PP-only	4.78 (1.5)	3.53 (2.1)	-0.59	5.08 (2.9)	3.57 (1.8)	-0.71	-0.57
Angular Velocity	MI-PP	334.5 (95.2)	365.6 (115.4)	0.30	370.7 (111.1)	364.2 (93.7)	-0.07	0.32
	PP-MI	289.1 (95.7)	350.9 (121.9)	0.55	359.8 (103.8)	360.3 (123.7)	0.01	0.63
	PP-only	328.9 (61.9)	347.5 (113.6)	0.21	334.2 (85.3)	348.9 (81.8)	0.18	0.28

Table 4.3

Linear mixed effects conducted to assess changes related to radial error.

	Radial error (cm)		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	12.45	7.82 – 17.07	**<0.001**
PP-MI	-0.37	-2.41 – 1.66	0.720
PP-only	0.43	-1.52 – 2.38	0.667
Day 5	0.22	-0.99 – 1.43	0.720
Day 6	-0.35	-1.56 – 0.86	0.573
Day 10	-2.49	-3.69 – -1.28	**<0.001**
Male	-2.26	-3.86 – -0.66	**0.006**
Age	-0.13	-0.31 – 0.05	0.168
PP-MI group : Day 5	-2.32	-4.04 – -0.59	**0.008**
PP-only group : Day 5	-3.41	-5.04 – -1.79	**<0.001**
PP-MI group : Day 6	-2.06	-3.79 – -0.34	**0.019**
PP-only group : Day 6	-1.23	-2.86 – 0.39	0.137
PP-MI group : Day 10	1.05	-0.68 – 2.77	0.234
PP-only group : Day 10	-0.59	-2.21 – 1.04	0.478
Random Effects			
σ^2	30.48		
$\tau_{00\ \mathrm{participantNum}}$	3.75		
ICC $_{\mathrm{participantNum}}$	0.11		
Observations	2091		
Marginal R^2 / Conditional R^2	0.076 / 0.177		

Table 4.4

Linear mixed effects conducted on kinematic outcomes to determine variables linked to radial error on the dart throwing task.

	Radial error (cm)		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	7.53	6.67 – 8.38	**<0.001**
Elbow angle at release	0.82	-0.11 – 1.76	0.085[†]
Elbow angle at take back	-0.29	-0.83 – 0.25	0.291
Shoulder angle at release	-0.68	-1.23 – -0.13	**0.015**[†]
Shoulder angle at take back	-0.69	-1.26 – -0.12	**0.018**[†]
Release time	-0.27	-1.10 – 0.57	0.530
Angular velocity	-0.57	-1.55 – 0.42	0.262
Random Effects			
σ^2	31.39		
$\tau_{00\ \text{participant}}$	5.89		
$\text{ICC}_{\text{participant}}$	0.16		
Observations	1840		
Marginal R^2 / Conditional R^2	0.034 / 0.187		

[†] Note: Stemming from these results, shoulder angle at both release and take back (statistically significant), as well as elbow angle at release (trending) were included in further analyses of global kinematic variability.

Following standard preprocessing procedures (Jenkinson et al., 2002; Smith et al., 2002; Andersson et al., 2003), between and within-group comparisons were conducted using statistical activation maps across runs for each individual and time point to characterise functional brain changes during MI of the dart throwing task. Table 4.5 reports within-group comparisons (pre vs. mid; mid vs. post), indicating that training-related changes in brain activation that achieved statistical significance were only driven via PP, and only in the early stages of learning. As all groups demonstrated similar improvements in performance over the course of the study, we also conducted a comparison pre/post (i.e., post- > pre-training scan) across all subjects, revealing greater activation localized to regions including bilateral precuneus, fusiform gyri, middle temporal gyri, and occipital regions at the post-training scan (post > pre; Fig 4.3; Table 4.6).

Between-group comparisons, adjusted for BVE, were conducted at each scan to assess the impact of training modality on resultant patterns of MI-related brain activity. At the pre-training scan, greater activation was observed for the MI-PP group, localized to the ipsilateral cerebellum (MI-PP > PP-MI; Table 4.7). At the mid-training scan, greater activation was observed for the PP MI (PP-MI > MI-PP), localized to regions including the SMA, anterior cingulate cortex, cerebellum, contralateral precentral and middle temporal gyri, and ipsilateral superior frontal gyrus. Negative correlations between BVE and MI-related activity were found in regions including bilateral parietal cortices and lingual gyri (Fig 4.4; Table 4.7). At the post-training scan, no differences that reached statistical significance were observed, but negative correlations between BVE and MI-related activity were found in regions including bilateral frontal and occipital regions (Table 4.7). Prior to conducting group-level comparisons, we generated MI vs. rest (i.e., task-positive) activation maps across all participants at each time point. MI-related activation was demonstrated in a number of regions, including bilateral frontal and temporal, contralateral precentral gyrus, and ipsilateral cerebellar regions (Hétu et al., 2013; Hardwick et al., 2018). These plots are included as Supplementary Materials (Appendix B; Figure 6.2).

Table 4.5

MNI coordinates of the local maxima resulting from comparisons conducted to assess within-group differences in MI-related brain activation following training of the dart throwing task.

	Anatomical region	MNI coordinates (mm)			Z-score
		x	y	z	
PP-MI group					
Mid > pre-training	L Middle temporal gyrus	-66	-14	-4	4.51
	L Thalamus	-4	-20	-7	4.38
	L Middle temporal gyrus	-62	-4	-8	4.34
	L Anterior cingulate	-14	49	-3	3.54
	L Middle frontal gyrus (orbital)	-18	57	-16	3.53
	L Medial orbitofrontal cortex	-10	56	-1	3.36
	R Supramarginal gyrus	44	-39	22	4.53
	R Supramarginal gyrus	46	-39	24	4.45
	R Supramarginal gyrus	49	-39	25	4.43
	R Medial frontal gyrus	6	38	54	3.65
	R Medial orbitofrontal cortex	9	59	0	3.51
	R Medial frontal gyrus	15	49	2	3.46
Pre > mid-training	-	-	-	-	-
Post </> mid-training	-	-	-	-	-
MI-PP group					
Mid </> pre-training	-	-	-	-	-
Post </> mid-training	-	-	-	-	-

Table 4.6

MNI coordinates of the local maxima of regions activated during MI of the dart throwing task across all participants. Comparisons were conducted to assess differences in MI-related brain activation following training.

Anatomical region		MNI coordinates (mm)			Z-score
		x	y	z	
Post > pre-training	L Precuneus	-12	-57	41	3.46
	L Fusiform gyrus	-31	-62	-13	3.38
	L Fusiform gyrus	-31	-58	-14	3.19
	L Fusiform gyrus	-36	-41	-24	2.92
	L Inferior occipital gyrus	-29	-75	-5	2.86
	L Inferior occipital gyrus	-30	-86	-7	2.83
	L Inferior occipital gyrus	-46	-81	-7	2.82
	L Middle temporal gyrus	-52	8	-26	3.93
	L Middle temporal gyrus	-57	-6	-8	3.68
	L Middle temporal gyrus	-57	9	-20	3.63
	L Middle temporal gyrus	-53	-11	-6	3.36
	L Middle temporal gyrus	-57	0	-18	3.15
	L Superior temporal gyrus	-54	-5	-8	3.68
	R Cuneus	18	-57	36	3.97
	R Precuneus	19	-50	41	3.46
	R Precuneus	19	-50	45	3.41
	R Precuneus	19	-50	47	3.35

	R Precuneus	12	-57	35	3.32
	R Superior occipital gyrus	27	-96	17	3.36
	R Superior occipital gyrus	26	-96	23	3.34
	R Superior occipital gyrus	28	-96	21	3.33
	R Superior occipital gyrus	14	-100	26	3.14
	R Fusiform gyrus	36	-61	-11	3.07
	R Fusiform gyrus	35	-59	-11	3.07
	R Middle temporal gyrus	54	-11	-11	3.77
	R Superior temporal gyrus	56	-10	-5	3.73
	R Middle temporal pole	32	18	-34	3.6
	R Middle temporal pole	52	12	-23	3.53
	R Middle temporal pole	50	12	-28	3.41
	R Superior temporal pole	38	10	-27	3.53

Note: no significant differences in activation were observed for pre > post-training.

Table 4.7

MNI coordinates of local maxima resulting from between-group comparisons conducted at each time point.

Anatomical Region			MNI coordinates (mm)			Z-score
			x	y	z	
Pre-training						
	MI-PP > PP-MI	R Cerebellum (lobule VI)	24	-59	-34	3.25
		R Cerebellum (lobule VIIb)	26	-77	-47	3.38
		R Cerebellum (lobule VIIb)	33	-69	-47	3.08
		R Cerebellum (lobule VIII)	22	-59	-37	3.13
		R Cerebellum (crus I)	39	-88	-32	2.85
		R Cerebellum (crus II)	28	-90	-40	3.12
	PP-MI > MI-PP	-	-	-	-	-
Mid-training						
	MI-PP > PP-MI	-	-	-	-	-
	PP-MI > MI-PP	L Superior temporal pole	-36	27	-26	3.73
		L Middle temporal gyrus	-67	-10	-2	3.53
		L Superior temporal pole	-46	3	-15	3.4
		L Middle temporal gyrus	-64	-12	-7	3.33
		L Superior temporal pole	-55	12	-10	3.27
		L Superior temporal pole	-56	9	-7	3.27
		L Cerebellum (lobule VI)	-26	-59	-29	3.22
		L Cerebellum (lobule VI)	-27	-62	-20	3.1
		L Cerebellum (lobule IV/V)	-4	-59	-18	3.06
		L Anterior cingulate	0	8	26	3.39

	L Medial frontal gyrus	-11	34	35	2.81
	L Anterior cingulate	-9	33	18	2.73
	L Precentral gyrus	-30	-16	76	3.23
	L SMA	-11	-5	73	3.22
	L SMA	-8	0	81	3.21
	L Paracentral lobule	-16	-20	77	3.13
	R Cerebellum (lobule IV/V)	10	-46	-7	3.2
	R Cerebellum (vermis IV/V)	4	-58	-16	3.1
	R Cerebellum (lobule IV/V)	11	-50	-7	2.93
	R Anterior cingulate	10	12	30	2.81
	R SMA	2	-3	58	2.73
	R SMA	2	3	52	2.71
	R Superior frontal gyrus	16	-3	74	3.11
	R Superior frontal gyrus	27	-5	68	3
Positive BVE effect	-	-	-	-	-
Negative BVE effect	L Superior parietal lobule	-18	-51	51	3.52
	L Superior parietal lobule	-17	-51	53	3.51
	L Precuneus	-18	-51	51	2.91
	L Lingual gyrus	-8	-59	53	3.34
	L Lingual gyrus	-19	-78	0	3.32
	L Lingual gyrus	-21	-78	1	3.32
	L Lingual gyrus	-21	-80	0	3.31
	L Calcarine	-20	-74	0	3.07
	R Superior parietal lobule	21	-66	64	3.45
	R Angular gyrus	40	-60	30	3.32

		R Superior parietal lobule	27	-56	66	3.02
		R Lingual Gyrus	19	-77	-1	3.05
Post-training						
	MI-PP >/< PP-MI	-	-	-	-	-
	Positive BVE effect	-	-	-	-	-
	Negative BVE effect	L Middle occipital gyrus	-46	-96	-3	4.42
		L Middle occipital gyrus	-45	-96	-7	4.35
		L Middle occipital gyrus	-43	-98	-8	4.32
		L Middle occipital gyrus	-47	-95	2	3.63
		L Cuneus	-5	-93	32	3.70
		L Middle frontal gyrus	-34	65	24	3.79
		L Superior frontal gyrus	-31	65	26	3.55
		L Superior frontal gyrus	-28	65	28	3.36
		R Inferior occipital gyrus	41	-75	-4	3.69
		R Middle frontal gyrus	30	68	26	4.22
		R Middle frontal gyrus	21	69	29	3.67
		R Middle frontal gyrus	32	58	30	3.58

Note: instances in which no significant differences in activation were noted are indicated by dashed lines.

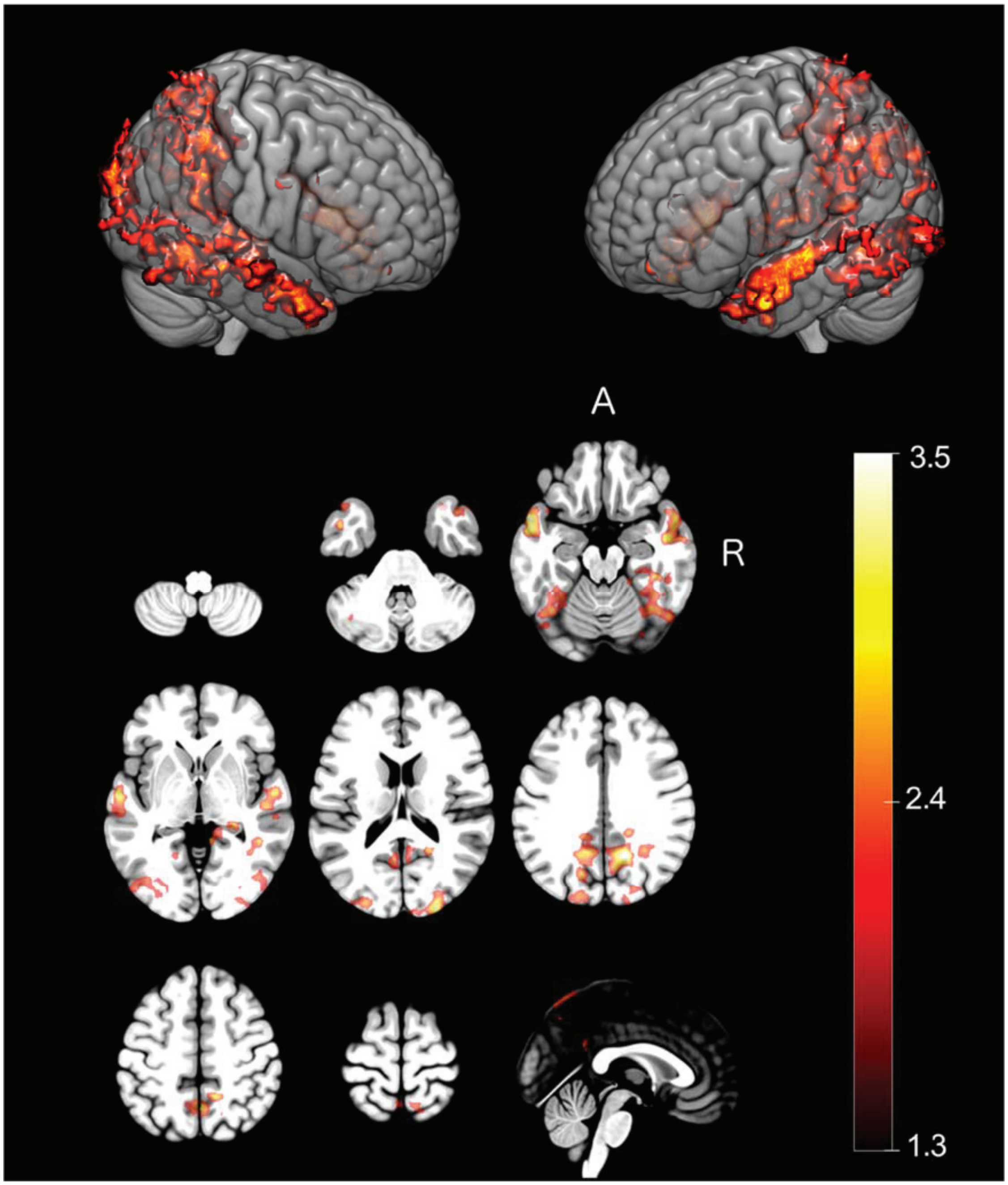


Figure 4.3 Effects of training on resultant motor imagery-based brain activity where the colourbar represents the Z-max value. Activated voxel clusters remaining after subtraction of the map of activations of post-training scan from the pre-training scan across all participants. Activation was localized to regions including bilateral fusiform gyri, precuneus, middle temporal gyri, and middle occipital gyri. Clusters shown reached a cluster corrected threshold ($Z>2.0$; $p < 0.05$), family-wise error corrected for number of comparisons, and are shown overlaid on the MNI template.

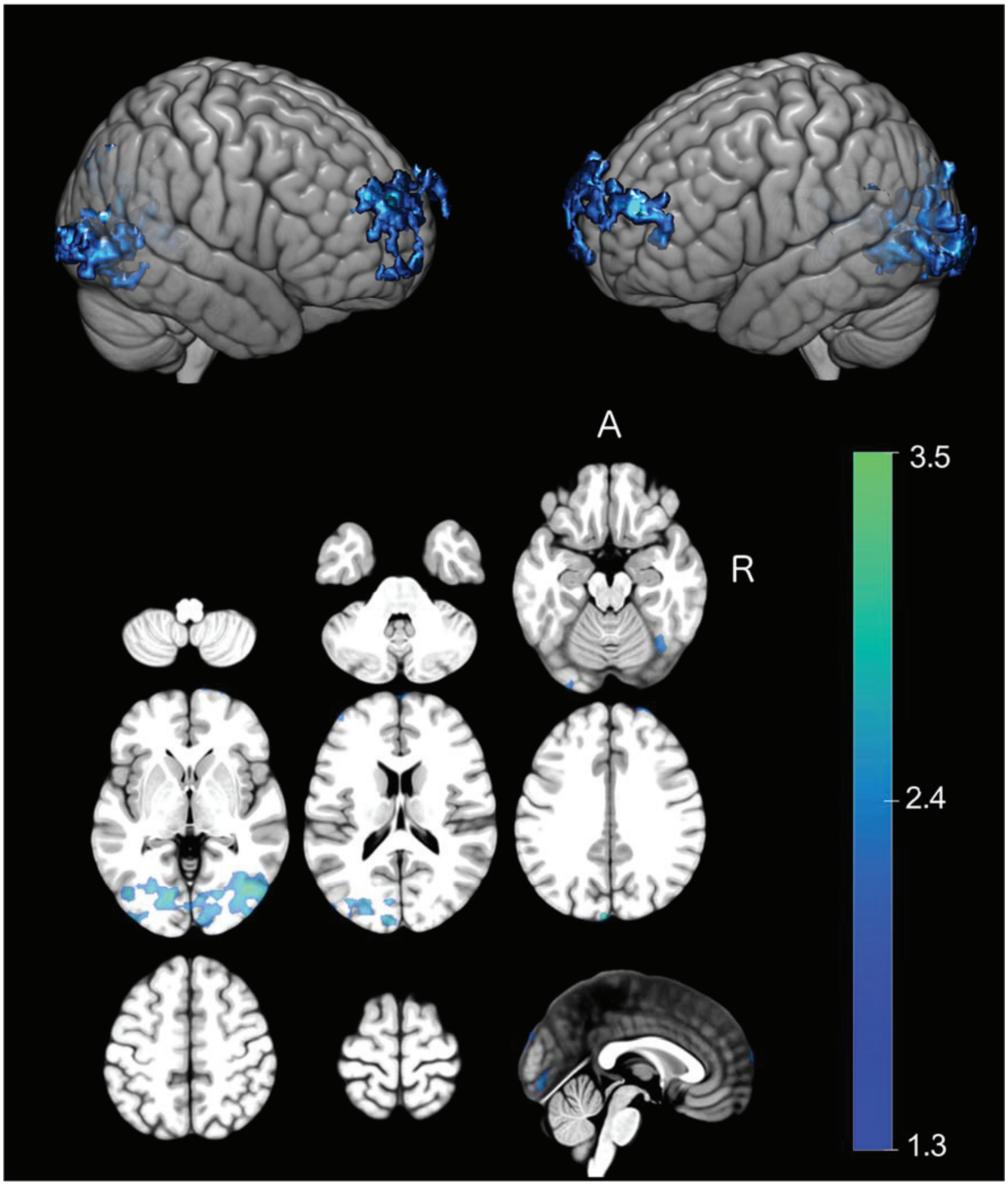


Figure 4.4 Correlation between brain activity and performance (bivariate variable error) at the post-training scan, where the colourbar represents the Z-max value. During motor imagery, bivariate variable error correlates negatively with brain activity localized to occipital regions as well as left superior and bilateral middle frontal gyri. Clusters shown reached a cluster corrected threshold ($Z>2.0$; $p < 0.05$), family-wise error corrected for number of comparisons, and are shown overlaid on the MNI template.

4.4 DISCUSSION

Here, we manipulated the order of MI and PP in training to test the prediction that the nature of MI lends itself to facilitating encoding of effector independent representations central to the cognitive stage of skill acquisition. Our findings improve upon theories posing that MI is analogous to PP – that drawing from shared neural substrates, a simulation of movement occurs (Jeannerod, 2001; Wakefield et al., 2013; Collins and Carson, 2017; O'Shea and Moran, 2017). Here, we provide unique information as to how a simulation of movement in the absence of feedback, is able to drive skill acquisition. In particular, we show that MI facilitates effector independent encoding central to early stages of skill acquisition, reflected in global vs. specific aspects of movements, and acts as scaffolding for which effector dependent encoding can be readily facilitated.

Our argument, that MI facilitates encoding of effector independent representations, arises from the finding that MI led to improvements in the global aspects of the movement (i.e., changes in consistency in performance, and global kinematics). Further, that these improvements were only observed when MI was applied prior to PP and following training (i.e., after all ten sessions). Improvement in consistency and overall movement efficiency or coordination amongst multiple joints/effectors (i.e., global kinematics) reflect the occurrence of effector independent encoding central to the early stages of skill acquisition (Land et al., 2016; Ingram et al., 2016; Kraeutner et al., 2017; Kraeutner et al., 2016a; Lohse et al., 2010a; Mizuguchi et al., 2014). Specifically, these improvements reflect the ongoing processing of environmental and sensory stimuli of the movement and integration with an understanding of movement elements and task goals to create a motor representation (Fitts and Posner, 1967; Verwey et al., 2015). While the admittedly small decrease in global kinematic variability observed when MI was applied following PP reflects ongoing updating of environmental and sensory information and minimal refinements to effector independent representations, these refinements do not translate to further improvements in task-related outcomes. In particular, we did not observe further improvements in consistency (or accuracy) when MI was applied following PP, once the motor program was mapped to an effector and had begun its refinement through PP. Additionally, we show that following an equivalent bout of training, greater overall gains in performance were observed when MI preceded PP vs. its alternative (i.e., when MI followed PP). Thus, effector independent representations facilitated through MI provide scaffolding for which these representations can be mapped to a specific effector.

Critically, these representations are not mapped to a specific effector through MI as we did not observe changes in specific aspects (i.e., RE or ACF1) of the movement driven via MI applied at any point in the study. Changes related to RE and the ACF1 reflect the onset of effector dependent encoding, whereby the changes observed from trial-trial represent the well-established error detection/correction mechanism that facilitates the ideal kinematics of the end-effector and allow for the task goal to be achieved (i.e., the final position of the dart; Todorov et al., 1997). Consequently, that MI is only able to process and integrate environmental and sensory information with movement goals, it follows that a decrease in RE was only driven following PP at any point in training and that ACF1 was only observed to improve in the second half of training (i.e., once mapping of the representations to a specific effector had occurred). Further support of this notion is derived from a body of evidence showing that MI, relative to PP, creates more complex structures of the mental representation a movement (i.e., a composition of a number of different movement ‘chunks’ termed basic action concepts that are organized into a hierarchical structure as expertise is gained; Schack, 2004; Frank et al., 2014; Frank and Schack, 2017). Specifically, as the enhanced complexity of these structures does not translate one-to-one at the behavioural level, the elaborateness of these structures can be directly linked to refinement of effector independent representations of the skill. Importantly, decreased activation localized to the supplementary motor area (SMA) and cerebellum at the mid-training scan (see Chapter 3) observed following an equivalent bout of MI- vs. PP-based training supports the notion that MI only facilitates effector independent encoding. Specifically, these regions are implicated in both the 'kinematics-to-dynamics' transform (Li et al., 2001; Padoa-Schioppa et al., 2002, 2004), reflecting the dynamics of the upcoming movement, and error detection/correction mechanisms that rely on sensory reafferance to update the motor program (Blakemore et al., 1998; Wolpert et al., 1998; Blakemore and Sirigu, 2003; Shadmehr et al., 2010; Shadmehr, 2018), and thus mapping of the motor program to the specific effector.

As alterations to the motor representation/program occur through internal comparisons (Miall and Wolpert, 1996; Wolpert et al., 1998; Bastian, 2006; Popa et al., 2012), how MI facilitates the development of these representations in the absence of feedback remains a key question. During PP, the predicted consequences of the movement (efference copy) are compared to actual movement outcomes (reafference) in a forward model to update the motor program (Miall and Wolpert, 1996; Wolpert et al., 1998; Bastian, 2006; Popa et al., 2012). Yet, while feedback is precluded in an error detection/correction mechanism without sensory information during MI, work supports the hypothesis that an alternative internal comparison is in play during motor imagery-based practice (O'Shea and Moran, 2017; Ehrsson et al., 2018; Ingram et al., 2019), as the motor program is shown to undergo training-related alterations during MI-based practice (Gentili et al., 2006, 2010; Kraeutner et al., 2016b; Ingram et al., 2019). Critically, prior work has shown that an internal comparison does not necessarily rely on sensory feedback (Dahm and Rieger, 2019). Specifically, by assessing predicted errors on a dart throwing task during MI and PP with either delayed or occluded visual feedback, no advantage was observed with the existence of somatosensory or visual feedback. Further, work showing that MI-based practice facilitated improvements in performance following five sessions of practice on a multi-articular tracing task that were greater than that observed for PP without visual feedback, led to the conclusion that the predicted consequences of the movement are compared to a simulated representation of the movement that produce a corresponding sensory representation (Ingram et al., 2019). However, this sensory representation is inferior to sensory feedback, as improvements in performance facilitated through MI remained inferior to that driven by PP with a reduced frequency of visual feedback (Wulf et al., 1995). Thus, actual execution, and in turn sensory feedback vs. a corresponding sensory representation, leads to the development of a stronger error detection and correction mechanism (Wulf et al., 1995).

In light of this aforementioned evidence, our neuroimaging findings indeed suggest a separate system underlies error detection and correction, to ultimately refine effector independent representations, driven via MI. While we did not observe changes in brain activation driven by MI-based practice at any point throughout the study, performance (BVE) on the darts task was shown to correlate negatively with brain activity localized to bilateral parietal cortices and lingual gyri at the mid-training scan (see Chapter 3), and with brain activity localized to occipital regions as well as left superior and bilateral middle frontal gyri at the post-training scan. Activation of these regions during imagery is thought to reflect the reliance on a visual image during imagery (Olsson et al., 2008). Interestingly, a system that comparing visual feedback to simulated visual consequences is critical to planning motor actions (during physical practice) prior to effector selection, separate from that which generates the efference copy and intended consequences of the movement

(Pilacinski et al., 2018). Thus, the visual image relied on during MI serves as the corresponding sensory feedback in alternative comparison involving this simulated visual and intended visual consequences of the movement, generated through a perceptual efference copy (Tian and Poeppel, 2010). This argument is substantiated by our finding that an increase in activation localized to regions including bilateral occipital cortices, middle temporal gyri, fusiform gyri, and precuneus was observed following training, in line with work demonstrating greater activation of occipital-temporal areas in expert vs. novice archers (Kim et al., 2008) and golfers (Milton et al., 2007) during their pre-shot routine. Activation of these regions, associated with task expertise, is thought to reflect greater visual control and perceptual learning (Gauthier et al., 2000; Milton et al., 2007; Kim et al., 2008); thus, greater activation within these regions during MI of the dart throwing task reflects a more established forward model that relies on a corresponding sensory representation (i.e., simulated visual feedback) vs. sensory reafferance. Of note, why we did not observe changes in MI-related brain activity driven in the second half of training is likely attributed to methodological limitations: namely, that BOLD indirectly reflects an increased use of neural substrates and is limited by its low temporal resolution (Sutton et al., 2009). Studies employing electrophysiological measures report both a smaller magnitude and shorter period of activation during motor imagery relative to physical practice of the same task (Burianová et al., 2013; Duann and Chiou, 2016; Kraeutner et al., 2014) . As we employed 30 sec blocks during the fMRI experiment, mirroring the blocks during training and testing, it is thus possible that any lasting changes in the MI-related brain activation driven by training may be too minimal or not sustained long enough to be observed via fMRI (Kraeutner et al., 2014; Pfurtscheller and Neuper, 1997). Further, as months or years of practice are required to acquire expertise of a dart-throwing task, and none of our participants achieved an expert-level of proficiency on the task, the changes driven in the second half of training may have been too minimal to be detected by our fMRI analyses.

Notably, this work has important implications for the way in which skill acquisition via MI is probed. That MI drives encoding of effector independent representations, but typical outcome measures are more suited to capturing effector dependent encoding, provides an explanation, at least in part, for the inconsistencies in performance gains driven through MI noted in the literature (see Di Rienzo et al., 2016 for a review). For instance, performance gains driven by MI are observed to be marginal when assessing specific task-related outcomes on complex motor tasks (e.g., accuracy on a dart throwing task as employed in Chapter 3; Di Rienzo et al., 2016). In contrast, robust gains in performance driven by motor imagery are observed in the wealth of literature employing key-press sequence tasks, whereby effector independent encoding is critical (Di Rienzo et al., 2016). Yet, performance of discrete key-presses (i.e., overall reaction times vs. sequence-specific) reflecting the motoric or effector-specific component is not observed following a bout of MI (Kraeutner et al., 2016b). As effector independent representations are transferrable across effectors, it is thus critical to consider the use of intermanual transfer tasks (similar to Wohldmann et al., 2007; Lohse et al., 2010a; Land et al., 2016) in addition to typical outcome measures, to probe skill acquisition driven via MI relative to PP.

In summary, we show that MI facilitates encoding of effector independent representations (reflected in improvements in global vs. specific aspects of movements) central to the early stages of skill acquisition. Further, while these representations are not mapped to specific effectors via MI, the encoding driven via MI acts as scaffolding for which effector dependent encoding can be readily facilitated through PP. Importantly, the way in which the development of effector independent representations is assessed is critical to consider in future investigations of MI-based skill acquisition.

4.5 REFERENCES

Akaike, H (1974). A new look at the statistical model identification. IEEE Trans. Automat. Contr., 19, 716–723.

Andersson J, Skare S, Ashburner J (2003) How to correct susceptibility distortions in spin-echo echo-planar images: application to diffusion tensor imaging. Neuroimage 20:870–888.

Bapi RS, Doya K, Harner AM (2000) Evidence for effector independent and dependent representations and their differential time course of acquisition during motor sequence learning. Exp Brain Res 132:149–162.

Bastian AJ (2006) Learning to predict the future: the cerebellum adapts feedforward movement control. Current opinion in neurobiology Available at: http://www.sciencedirect.com/science/article/pii/S0959438806001395.

Bates, D., Maechler, M., Bolker, B. (2015) Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1), 1-48.

Burianová H, Marstaller L, Sowman P, Tesan G, Rich A, Williams M, Savage G, Johnson B (2013) Multimodal functional imaging of motor imagery using a novel paradigm. NeuroImage 71:50–58.

Cohen A, Ivry R, Keele S (1990) Attention and structure in sequence learning. Journal of Experimental Psychology: Learning, Memory, and Cognition 16:1730.

Collins D, Carson H (2017) The future for PETTLEP: a modern perspective on an effective and established tool. Curr Opin Psychology 16:12–16.

Dahm S, Rieger M (2019) Is imagery better than reality? Performance in imagined dart throwing. Hum Movement Sci 66:38–52.

Di Rienzo F, Debarnot U, Daligault S, Saruco E, Delpuech C, Doyon J, Collet C, Guillot A (2016) Online and Offline Performance Gains Following Motor Imagery Practice: A Comprehensive Review of Behavioral and Neuroimaging Studies. Front Hum Neurosci 10:315.

Duann J-RR, Chiou J-CC (2016) A Comparison of Independent Event-Related Desynchronization Responses in Motor-Related Brain Areas to Movement Execution, Movement Imagery, and Movement Observation. PLoS ONE 11:e0162546.

Edwards B, Waterhouse J, Atkinson G, Reilly T, Edwards B, Waterhouse J, Atkinson G, Reilly T (2007) Effects of time of day and distance upon accuracy and consistency of throwing darts. Journal of Sports Sciences 25:1531–1538.

Fitts, P. M., Posner, M. I. (1967). Human performance. Belmont, CA: Brooks/Cole.

Frank C, Land WM, Popp C, Schack T (2014) Mental representation and mental practice: experimental investigation on the functional links between motor memory and motor imagery. PLoS ONE 9:e95175.

Frank C, Schack T (2017) The Representation of Motor (Inter)action, States of Action, and Learning: Three Perspectives on Motor Learning by Way of Imagery and Execution. Front Psychol 8:678.

Gauthier I, Skudlarski P, Gore JC, Anderson AW (2000) Expertise for cars and birds recruits brain areas involved in face recognition. Nat Neurosci 3:191–197.

Gentili R, Han CE, Schweighofer N, Papaxanthis C (2010) Motor learning without doing: trial-by-trial improvement in motor performance during mental training. J Neurophysiol 104:774–783.

Gentili R, Papaxanthis C, Pozzo T (2006) Improvement and generalization of arm motor performance through motor imagery practice. Neuroscience 137:761–772.

Grafton ST, Hazeltine E, Ivry RB (1998) Abstract and effector-specific representations of motor sequences identified with PET. J Neurosci 18:9420–9428.

Gregg M, Hall C, Butler A (2010) The MIQ-RS: A Suitable Option for Examining Movement Imagery Ability. Evid Based Complement Alternat Med 7:249–257.

Gregg M, Hall C, Nederhof E (2005) The imagery ability, imagery use, and performance relationship. The Sport Psychologist 19:93–99.

Grèzes J, Decety J (2001) Functional anatomy of execution, mental simulation, observation, and verb generation of actions: a meta-analysis. Hum Brain Mapp 12:1–19.

Hancock GR, Butler MS, Fischman MG (1995) On the Problem of Two-Dimensional Error Scores: Measures and Analyses of Accuracy, Bias, and Consistency. J Mot Behav 27:241–250.

Hardwick RM, Caspers S, Eickhoff SB, Swinnen SP (2018) Neural correlates of action: Comparing meta-analyses of imagery, observation, and execution. Neurosci Biobehav Rev 94:31–44.

Hétu S, Grégoire M, Saimpont A, Coll M-P, Eugène F, Michon P-E, Jackson P (2013) The neural network of motor imagery: An ALE meta-analysis. Neuroscience and biobehavioral reviews 37:930–949.

Ingram TG, Kraeutner SN, Solomon JP, Westwood DA, Boe SG (2016) Skill acquisition via motor imagery relies on both motor and perceptual learning. Behav Neurosci 130:252–260.

Ingram TGJG, Solomon JP, Westwood DA, Boe SG (2019) Movement related sensory feedback is not necessary for learning to execute a motor skill. Behav Brain Res 359:135–142.

Jeannerod M (2001) Neural Simulation of Action: A Unifying Mechanism for Motor Cognition. NeuroImage 14:S103–S109.

Jenkinson M, Bannister P, Brady M, Smith S (2002) Improved optimization for the robust and accurate linear registration and motion correction of brain images. Neuroimage 17:825–41.

Kilteni K, Andersson BJ, Houborg C, Ehrsson HH (2018) Motor imagery involves predicting the sensory consequences of the imagined movement. Nat Commun 9:187.

Kim J, Lee H, Kim W, Park H, Kim S, Moon D, Woo M, Tennant L (2008) Neural correlates of pre-performance routines in expert and novice archers. Neurosci Lett 445:236–241.

Kraeutner S, Gionfriddo A, Bardouille T, Boe S (2014) Motor imagery-based brain activity parallels that of motor execution: Evidence from magnetic source imaging of cortical oscillations. Brain research 1588:81–91.

Kraeutner SN, Ingram TGJG, Boe SG (2017) The effector independent nature of motor imagery: Evidence from rTMS induced inhibition to the primary motor cortices. Neuropsychologia 97:1–8.

Kraeutner SN, Keeler LT, Boe SG (2016a) Motor imagery-based skill acquisition disrupted following rTMS of the inferior parietal lobule. Experimental brain research 234:397–407.

Kraeutner SN, MacKenzie LA, Westwood DA, Boe SG (2016b) Characterizing skill acquisition through motor imagery with no prior physical practice. Journal of experimental psychology Human perception and performance 42:257–265.

Land WM, Liu B, Cordova A, Fang M, Huang Y, Yao WX (2016) Effects of Physical Practice and Imagery Practice on Bilateral Transfer in Learning a Sequential Tapping Task. PLoS ONE 11:e0152228.

Lohse K, Healy A, Sherwood D (2010a) Mental Practice in the Intermanual Transfer of Motor Skills. J Imag Res Sport Phys Activity 5:6.

Lohse KR, Sherwood DE, Healy AF (2010b) How changing the focus of attention affects performance, kinematics, and electromyography in dart throwing. Hum Mov Sci 29:542–555.

MacKay D (1982) The problems of flexibility, fluency, and speed–accuracy trade-off in skilled behavior. Psychol Rev 89:483.

Miall RC, Wolpert DM (1996) Forward Models for Physiological Motor Control. Neural Networks 9:1265–1279.

Milton J, Solodkin A, Hluatík P, Small S (2007) The mind of expert motor performance is cool and focused. NeuroImage 35:804–813.

Mizuguchi N, Nakata H, Kanosue K (2014) Effector-independent brain activity during motor imagery of the upper and lower limbs: an fMRI study. Neurosci Lett 581:69–74.

Moran A, Guillot A, MacIntyre T, Collet C (2012) Re-imagining motor imagery: Building bridges between cognitive neuroscience and sport psychology: Re-imagining motor imagery. British Journal of Psychology 103:224–247.

Nelson-Wong E, Howarth S, Winter DA, Callaghan JP (2009) Application of autocorrelation and cross-correlation analyses in human movement and rehabilitation research. J Orthop Sports Phys Ther 39:287–295.

O'Shea H, Moran A (2017) Does Motor Simulation Theory Explain the Cognitive Mechanisms Underlying Motor Imagery? A Critical Review. Front Hum Neurosci 11:72.

Oldfield RC (1971) The assessment and analysis of handedness: The Edinburgh inventory. Neuropsychologia 9:97113.

Olsson C-JJ, Jonsson B, Larsson A, Nyberg L (2008) Motor representations and practice affect brain systems underlying imagery: an FMRI study of internal imagery in novices and active high jumpers. Open Neuroimag J 2:5–13.

Pfurtscheller G, Neuper C (1997) Motor imagery activates primary sensorimotor area in humans. Neuroscience Letters 239:6568.

Pilacinski A, Wallscheid M, Lindner A (2018) Human posterior parietal and dorsal premotor cortex encode the visual properties of an upcoming action. Plos One 13:e0198051.

Popa LS, Hewitt AL, Ebner TJ (2012) Predictive and feedback performance errors are signaled in the simple spike discharge of individual Purkinje cells. J Neurosci 32:15345–15358.

Querfurth S, Schücker L, de Lussanet M, Zentgraf K (2016) An Internal Focus Leads to Longer Quiet Eye Durations in Novice Dart Players. Frontiers Psychology 7:633.

Schack T (2004) The cognitive architecture of complex movement. Int J Sport Exerc Psychology 2:403–438.

Schorer J, Jaitner T, Wollny R, Fath F, Baker J (2012) Influence of varying focus of attention conditions on dart throwing performance in experts and novices. Exp Brain Res 217:287–297.

Schuster C, Hilfiker R, Amft O, Scheidhauer A, Andrews B, Butler J, Kischka U, Ettlin T (2011) Best practice for motor imagery: a systematic literature review on motor imagery training elements in five different disciplines. BMC medicine 9:75.

Sherwood DE, Lohse KR, Healy AF (2014) Judging joint angles and movement outcome: Shifting the focus of attention in dart-throwing. J Exp Psychol Hum Percept Perform 40:1903–1914.

Smeets JB, Frens MA, Brenner E (2002) Throwing darts: timing is not the limiting factor. Experimental Brain Research 144:268–274.

Smith S (2002) Fast robust automated brain extraction. Human Brain Mapping 17:143–155.

Smith SM, Jenkinson M, Woolrich MW et al (2004) Advances in functional and structural MR image analysis and implementation as FSL. Neuroimage 23(Suppl 1):S208–S219.

Stinear C, Byblow W, Steyvers M, Levin O, Swinnen S (2006) Kinesthetic, but not visual, motor imagery modulates corticomotor excitability. Experimental Brain Research 168:157–164.

Sutton B, Ouyang C, Karampinos D, Miller G (2009) Current trends and challenges in MRI acquisitions to investigate brain function. International Journal of Psychophysiology 73:33–42.

Tian X, Poeppel D (2010) Mental imagery of speech and movement implicates the dynamics of internal forward models. Auditory Cognitive Neurosci 1:166.

Todorov E, Shadmehr R, Bizzi E (1997) Augmented Feedback Presented in a Virtual Environment Accelerates Learning of a Difficult Motor Task. J Mot Behav 29:147–158.

Tyč F, Boyadjian A (2011) Plasticity of motor cortex induced by coordination and training. Clin Neurophysiol 122:153–162.

Van Beers RJ (2009) Motor learning is optimally tuned to the properties of motor noise. Neuron 63:406–417.

Van Beers RJ, van der Meer Y, Veerman RM (2013) What autocorrelation tells us about motor variability: insights from dart throwing. PLoS ONE 8:e64332.

Verwey WB, Shea CH, Wright DL (2015) A cognitive framework for explaining serial processing and sequence execution strategies. Psychon Bull Rev 22:54–77.

Wakefield C, Smith D, Moran A, Holmes P (2013) Functional equivalence or behavioural matching? A critical reflection on 15 years of research using the PETTLEP model of motor imagery. Int Rev Sport Exer P 6:105–121.

Wohldmann EL, Healy AF, Lyle BEJ (2007) Pushing the limits of imagination: Mental practice for learning sequences. Journal of Experimental Psychology: Learning, Memory, and Cognition 33:254261.

Wolpert DM, Miall RC, Kawato M (1998) Internal models in the cerebellum. Trends Cogn Sci (Regul Ed) 2:338–347.

World Darts Federation (2017): WDF Playing and Tournament Rules July 25, 2017. Available from: URL: http://www.dartswdf.com/rules/.

Wulf G, Horstmann G, Choi B (1995) Does Mental Practice Work like Physical Practice without Information Feedback? Res Q Exercise Sport 66:262–267.

Chapter 5 : GENERAL DISCUSSION

5.0 SUMMARY OF FINDINGS BY CHAPTER

This thesis sought to provide new knowledge related to the neural mechanisms of MI and nature of MI-based skill acquisition. Each experiment, presented in Chapters 2-4, addressed a relevant question pertaining to the mechanisms underlying MI that had not been previously considered in the motor skill acquisition literature. Namely, this thesis asked the following research questions: 1) how does expertise modulate brain activity driven via MI?; 2) how does the modality in which the individual practices (MI vs. PP) modulates changes in both performance and MI-based brain activity?: and 3) does MI rely on effector independent encoding to drive skill acquisition? The main findings from each chapter are summarized below.

Chapter 2: The primary aim of this chapter was to determine how expertise modulates brain activity driven via MI. During MI, novice performance is associated with widespread activity resembling novice physical performance, encompassing bilateral frontal and parietal regions. While the impact of task complexity on MI-related brain activation remains an important avenue of future research, the findings of this chapter provide insight regarding the importance of task selection when examining the neural correlates of MI. In particular, as many tasks employed in the MI literature to elucidate the neural correlates of MI employ skills for which the participant has limited expertise or experience, the resulting patterns of brain activity reflect a novice level of MI performance in addition to differences between MI and PP. Thus, work investigating MI-related brain activation should consider the level of expertise or experience of participants when selecting the task used in studies of MI.

Chapter 3: Building on work conducted in Chapter 2, as expertise was gained primarily through PP and no conclusions can be drawn in regard to the extent to which practice modality contributed to the achieved level of expertise (or the extent to which MI was used to facilitate learning is unknown), the primary aim of this chapter was to determine how the modality in which expertise of a complex motor skill is gained (i.e., MI vs. PP) manifests in resultant patterns of brain activity and performance after equivalent bouts of training. Here we show that relative to PP, MI-based training did not drive robust changes in brain activation and was inferior for realizing improvements in performance: greater activation in regions critical to refining the motor program were observed in the PP vs. MI group post-training, and MI led to smaller improvements in performance relative to PP. Critically, findings from this chapter provide unique knowledge related to the mechanism underlying MI-based skill acquisition, namely that 1) refinement of the motor program is less robust in MI owing to a difference in the mechanism underlying learning; and 2) different information is encoded in MI relative to PP.

Chapter 4: Building on the knowledge gained in Chapter 3, whereby noted disparities in resultant patterns of brain activation and performance outcomes between the two practice modalities led to the notion that information encoded during MI lends itself to the early stage of learning, the primary aim of this chapter was to examine the nature of information encoded in MI relative to PP by manipulating the stage that MI was applied in training of a complex motor skill.. Here, we show that MI drives changes in global aspects of a movement, reflecting effector independent encoding central to early stages of skill acquisition. Further, that these improvements were only observed when MI was applied prior to PP and following training (i.e., after all ten sessions) indicates that the encoding driven via MI acts as scaffolding for which effector dependent encoding can be readily facilitated. Additionally, findings from this chapter providing unique information as to how a simulation of movement in the absence of feedback is able to drive skill acquisition, improving upon theories posing that MI is analogous to PP.

Overall, the research outlined in this thesis addresses a diverse but related set of theoretical investigations pertaining to the mechanisms underlying MI, that have deeper implications for our understanding of both the neural underpinnings of MI and the application of MI for skill acquisition. Below, findings from the present work are discussed in the context of theories of MI – namely, that MI relies on shared neural substrates with PP to facilitate a simulation of movement without actual execution (Holmes and Collins, 2001; Jeannerod, 2001; O'Shea and Moran, 2017) – and the broader motor learning literature.

5.1 EXPERTISE-RELATED BRAIN ACTIVATION

The experiment presented in Chapter 2 utilized a within and between-group design to address limitations noted in prior work whereby only expertise of the participants is manipulated to assess the degree to which expertise is reflected in MI-related brain activation. In particular, we manipulated both the degree of (physical) expertise that participants had with each task as well as the expertise of the participants. The study presented in this chapter was largely motivated by confounds reported in the MI neuroimaging literature, whereby patterns of brain activity observed during MI are noted to be more widespread, encompassing a number of bilateral regions relative to PP (Milton et al., 2007; Chang et al., 2010; Debarnot et al., 2014). Yet, the degree to which these patterns resembled novice performance (i.e., in that they were driven by the novelty of the task itself, as many tasks employed in investigations of MI-related brain activation are novel) was unknown. Findings from this study have important implications for how the neural underpinnings of MI relative to PP are interrogated: novelty associated with the skill being performed in the scanner (through MI or PP) should be taken into consideration when evaluating resultant patterns of brain activation. Collectively, our findings and others suggest that changes in neural activity following training reflects greater efficiency of neural function (Milton et al., 2007; Haufler et al., 2000; et al., 2008; Del Percio et al., 2010; Bar and DeSouza, 2016; Guo et al., 2017), in that the reliance on regions underlying executive or higher cognitive functions is reduced as the motor program becomes consolidated, forward model capabilities are established, and the skill is carried out autonomously with less ‘effort’ (Milton et al., 2007; Percio et al., 2008; Del Percio et al., 2010; Yang, 2015; Guo et al., 2017).

While work in Chapter 3 provides further evidence in support of the notion that expertise is reflected in MI-related activation – that MI-related brain activation of a dart throwing task was modulated following training on the task – an increase in activation was observed localized to primarily bilateral frontal and posterior parietal regions following (physical) training. Following work by Bar and De Souza (2016), who showed a “U-shaped” pattern of brain activity (localized to their specific ROIs, the SMA and auditory cortex), during MI in professional ballet dancers over eight months of training on a new dance, the increase in cortical activation (vs. decrease) observed is likely attributed to the level of skill proficiency achieved at the post-training scan; in particular, none of our participants achieved expertise after five days of training, and were thus likely in the stage of learning whereby greater cognitive resources are required to understand task goals and consolidate the motor program (Yarrow et al., 2009; Dayan and Cohen, 2011; Bar and DeSouza, 2016). As pointed out in Guo et al., (2017), longitudinal studies examining the evolution of brain activity (either PP or MI-related) as expertise is achieved are lacking in the literature, and our understanding of the neural underpinnings of motor learning stem primarily from simple tasks typically employed in neuroimaging studies (i.e., key-press sequence tasks) that do not generalize well to complex or everyday motor tasks (Wulf and Shea, 2002). Thus, further research is required to determine how the stages of skill acquisition (and in particular, later stages) are reflected in the patterns of neural activity. Critically however, findings of the current work have implications for the broader body of motor learning literature – namely that further support is provided for the use of MI to probe learning of complex motor skills, as many of these skills cannot be performed in a scanner (Ross et al., 2003; Baeck et al., 2012; Bar and DeSouza, 2016).

5.2 INTERNAL MODELS IN MOTOR IMAGERY

Our findings from Chapter 3 (in conjunction with Chapter 4) have implications for the deeper investigation of the mechanism that underlies skill acquisition via MI in the absence of sensory feedback. As outlined in Chapter 4, it is likely that a separate system subserves internal comparisons for error detection/correction during MI. Yet, it is likely that these comparisons still rely on forward model processes as prior work has demonstrated the generation of an efference copy during MI (Kilteni et al., 2018; Dahm and Rieger, 2019). In an elegant study by Kilteni and colleagues (2018), whether or not intended consequences of a movement are predicted during MI through the generation of an efference copy was examined using a modified sensory attenuation (force-matching) paradigm. Specifically, perceived intensity of an external stimulus applied to the left index finger was assessed while participants simultaneously imagined (i.e., MI condition) pressing their right index finger against their left index finger, or remained relaxed (i.e., baseline condition, see Fig. 1.15). Typically, a self-generated touch is perceived as less intense when compared with an external force of identical intensity as the sensory consequences of the self-generated touch have already been predicted by the forward model based on the efference copy of the movement, resulting in attenuated sensory feedback. In this study, as the external stimulus was perceived as less intense during the MI condition relative to baseline, it was posited that this sensory attenuation during MI was due to a sensory prediction being generated (i.e., from the efference copy), and the authors concluded that sensory predictions occur during MI similarly to PP (Kilteni et al., 2018). The generation of an efference copy in MI is further supported by work from Dahm and colleagues, who employed a dart throwing task whereby participants predicted errors during MI or PP with either delayed or occluded visual feedback to probe whether or not intended consequences of the movement are predicted in MI. As no advantage was observed with the existence of somatosensory or visual feedback, they concluded that an internal simulation of action consequences must be occurring during MI and that this simulation did not rely on sensory reafference. In light of work showing that MI-based practice facilitated improvements in performance following five sessions of practice on a multi-articular tracing task that were greater than that observed for physical practice without visual feedback, it is likely that an alternative internal comparison is occurring during MI that does not rely on sensory reafference, and is instead suggested to involve a simulated feedback representation (Kilteni et al., 2018; Dahm and Rieger, 2019; Ingram et al., 2019). Yet, a key question regarding how this feedback representation is generated or the processes involving in the internal comparison occurring during MI remains elusive in the literature.

Here, stemming from our findings in light of evidence outlined below, we suggest that the feedback representation in MI is generated through long-term memory retrieval processes, which acts as a simulated visual consequence of the movement that are then compared to the efference copy of the movement in a separate error detection/correction system (i.e., a system not localized to the cerebellum as in PP). Pilot work by Zhang and colleagues (2019) demonstrated an increase in cortical activation localized primarily to dLPFC, PMC, and SMA when elite race walkers performed MI of their sport relative to recreational controls. In line with work suggesting that MI is knowledge-driven, relying on internal stimuli stored in long-term memory (Holmes and Calmels, 2008; Kim et al., 2017), the authors suggested that the increase in cortical activation was linked to well-developed feedforward capabilities, and that the elite athletes were relying on greater cognitive resources to draw upon the rich race-walking related information stored in their long-term memory for (alternative) forward model comparisons during MI (Zhang et al., 2019). While the increase in cortical activation is seemingly contrary to literature showing decreased MI-related activity as a function of skill expertise (i.e., as reported in Chapter 2), it is likely that greater resources were drawn upon as participants were asked to perform MI of the physical feeling of race walking vs. a discrete movement (Solodkin, 2004; Milton et al., 2007, 2008; Chang et al., 2010). However, if MI relies on retrieval processes to generate feedback representations, it follows that regions underlying memory retrieval would be more active during MI vs. PP of a trained task, as the availability of external information during PP would preclude the reliance on long-term memory. Indeed, activation localized to the temporal lobe and anterior cingulate, implicated in the retrieval of spatial and temporal information (Nyberg et al., 1996; Hayes et al., 2004), is increased during MI relative to PP of a sequence task following training (Lafleur et al., 2002; Lacourse et al., 2005).

Interestingly, work by Rieger and Massen (2014), where participants performed MI and PP (with and without visual feedback) of a novel colouring task, demonstrated the extent to which memory-related processes contribute to visual feedback generated during MI. During PP without visual feedback, participants were required to rely on memory to keep track of the parts of the image that they had 'already coloured' and the final product (as participants had to imagine the visual feedback). Notably, greater similarities were observed between MI and PP without visual feedback relative to PP with visual feedback (as assessed via mental chronometry). Thus, it was suggested that a similar process – that visual feedback was generated through retrieval processes – may also be occurring in MI. While learning was not assessed in this study, it is therefore reasonable to suggest that this mechanism subserves the generation of a visual feedback representation for the purposes of comparison with the efference copy for error detection/correction in MI (Rieger and Massen, 2014). Indeed, as reported in Chapter 4, activity localized to occipital regions, as well as middle frontal gyri (implicated in long-term memory retrieval of location information; Nyberg et al., 1996; Hayes et al., 2004) correlated negatively with performance on the darts task. Work by Tian and Poeppel (2010), who sought to discern between internal comparisons between auditory (perceptual) consequences of a movement vs. motor consequences, supports the existence of a separate system that involves a comparison of perceptual vs. motor representations. Specifically, the authors employed MEG to assess imagined practice of speech vs. MI of a simple key-press task relative to actual performance of both tasks. While limited in that they assessed temporal differences in amplitude (vs. a finer-grain spatial approach), they showed that patterns of activation localized to auditory regions supported an internal comparison for perceptual (i.e., speech) estimations with auditory consequences, distinct from somatosensory estimations with motor consequences (i.e., key-press; Tian and Poeppel, 2010). The kinesthetic feeling during MI was also linked to activity localized to posterior parietal regions (Tian and Poeppel, 2010), explaining previous findings demonstrating increased parietal activity with expertise (Hikosaka et al., 2002; Milton et al., 2007; Tian and Poeppel, 2010; Dayan and Cohen, 2011; Debarnot et al., 2014; Yang, 2015). Thus, in the context of the current work, it is reasonable to postulate that patterns of activation localized to visual regions may support an internal comparison between the efference copy and a visual feedback representation during MI. However, while we suggest this framework for which internal comparisons occur in MI to drive alterations to the motor representation, further research is necessary to determine the neural substrates that support an error detection/correction mechanism in MI.

5.3 TASK SPECIFICITY IN THE MI-LITERATURE

Collectively, this work has important implications for the way in which skill acquisition via MI is probed. As outcome measures typically used in studies of MI are more suited to capturing effector dependent encoding, that MI drives encoding of effector independent representations provides an explanation, at least in part, for the inconsistencies in performance gains driven through MI noted in the literature (see Di Rienzo et al., 2016 for a review). For instance, our findings showing that MI did not drive robust improvements in specific movement parameters is seemingly contrary to literature employing sequence tasks, whereby a bout of MI-based practice is shown to facilitate faster RTs (indicative of learning) to the trained vs. untrained sequence (see Nyberg et al., 2006; Wohldmann et al., 2007; Kraeutner et al., 2016, 2017 for examples) as well as greater lateralization of brain activation (Lacourse et al., 2004, 2005; Ono et al., 2013; et al., 2014). Arguably however, the extent to which the motor component must be 'learned' in a sequence task is minimal. As previously stated, the effector independent nature of MI lends itself to facilitating mapping of perceptual cues to movement goals – a key aspect of sequence learning. Thus, the decrease in RTs observed in the sequence literature may be driven primarily by this perceptual mapping, reflecting purely effector independent encoding. Yet, due to the greater reliance on effector independent encoding in sequence learning tasks, a robust behavioural improvement is observed following MI-based training. Findings from prior neuroimaging work supports this notion, as changes in brain activation driven through MI associated with sequence tasks are reported within frontal and parietal areas that support effector independent encoding (i.e., areas localized to the dorsal stream that subserve visually-guided actions and facilitates visuospatial processes; Rizzolatti and Matelli, 2003; Buxbaum et al., 2005, 2006, 2007; Binkofski and Buxbaum, 2013; Rizzolatti et al., 2014) vs. regions that support effector dependent encoding (Lacourse et al., 2005; Olsson et al., 2008; Zhang et al., 2012, 2016; Kraeutner et al., 2014; Hardwick et al., 2018; Hétu et al., 2013). Thus, it is critical to employ outcome measures that capture effector independent encoding when assessing MI-based skill acquisition.

As effector independent representations are transferrable across effectors, the use of intermanual transfer tasks (e.g., similar to Amemiya et al., 2010; Lohse et al., 2010; Ingram et al., 2016; Land et al., 2016) in addition to typical outcome measures, may be ideal in probing improvements in performance driven via MI. Indeed, similar improvements in performance for both the untrained and trained effector for simple unimanual (i.e., sequence or rotary pursuit) tasks has been observed (Land et al., 2016; Kohl and Roenker, 1980, 1983; Amemiya et al., 2010; Ingram et al., 2016), demonstrating the development of effector independent representations. Notably, Lohse et al., (2010) assessed intermanual transfer of a handwriting task following MI-based training. Improvements in production time were observed following MI, yet no improvements in the accuracy of the characters (as determined by size, as smaller size was taken to be indicative of improved accuracy) with the untrained effector. Researchers concluded that MI was unable to translate the motor representation to concrete patterns of muscle activation, and that while MI improved organization of the sequence of movements required to complete the task, effector dependent encoding did not occur. Importantly however, in assessing the improvements in performance achieved via the untrained effector, researchers were able to characterise the extent to which effector independent encoding occurred. Taking the above together, it is important to consider the perceptual vs. motor nature of the task employed in future investigations of MI-based skill acquisition, as well as the way in which improvements in performance are assessed. In particular, as MI-based practice does not translate at a one-to-one level behaviourally in the same way as PP (Wohldmann et al., 2007; Lohse et al., 2010; Frank et al., 2015; Frank and Schack, 2017), the use of intermanual transfer tasks to probe the development of effector independent representations facilitated via MI may provide greater sensitivity when assessing behavioural outcomes of MI-based practice.

5.4 SKILL TRANSFER FOLLOWING MI

Alternatively, effector independent encoding may further be probed by the use of skill transfer tasks. In particular, in line with prior theories of learning transfer, positive transfer is observed when skills share context and elements (Woodworth and Thorndike, 1901) or when processes underlying learning are shared (i.e., "transfer appropriate processing"; Lee, 1988). That MI facilitates effector independent encoding, relying on visuospatial processes, these visuospatial elements may transfer across domains (Rienhoff et al., 2013). For instance, Rienhoff et al. (2013), compared the extent to which basketball expertise (gained through PP) transferred to dart throwing using a between-group design involving novice and skilled basketball athletes. Skill transfer was assessed in terms of the ‘quiet eye’ (i.e., final fixation that occurs prior to task execution that occurs for a minimum of 100ms) duration, linked to superior performance (Vickers, 1996; Zentgraf et al., 2009), and accuracy on both tasks. Expert basketball players demonstrated greater accuracy on the darts task relative to the novices, yet no differences were observed for the quiet eye outcome. While the extent to which MI may facilitate skill transfer related to these task outcomes was not assessed in the study as the skilled basketball players obtained their expertise through PP, it is reasonable to suggest that MI may facilitate greater transfer of shared movement features relative to PP due to its reliance on effector independent encoding.

To explore this question, in the study reported in Chapter 4 we further employed a transfer task whereby all participants engaged in a golf putting test block similar to the dart throwing test blocks (see Appendix C for details). Both dart throwing and golf putting have a number of shared context and elements: both are transitive (with or towards an object), multi-joint and require fine motor control and visuomotor integration. Thus, visuospatial elements shared across both tasks show enhanced transfer across domains when training involved MI vs. when training strictly occurred through PP. Participants were instructed to putt the golf ball at a target on an artificial putting green, whereby points was the primary outcome measure (using a ring-based system; Smith et al., 2008). Group-level statistical analyses revealed an effect of time point, indicating that all groups did improve on this task, yet no differences between groups reached statistical significance (see Appendix C for details). However, while no advantage was observed for MI-based training vs. an equivalent bout of PP at acquisition or retention (day 1 vs. 5 and day 1 vs. 6, respectively) effect sizes conducted for the overall data (i.e., day 1 vs. 10), indicated that groups that employed MI during training led to an advantage on the transfer task as shown via large effect sizes for these groups relative to a moderate effect size obtained in the PP-only group (Appendix C). While the sensitivity of the outcome measure on the putting task was limited, our findings indicate that employing MI during training (at any point) leads to greater transfer of mechanisms and shared skill elements relative to PP. Thus, employing transfer tasks to characterise MI-based skill acquisition remains an important avenue of future research.

5.5 APPLICATION OF MOTOR IMAGERY IN STROKE REHABILITATION

Providing unique knowledge related to the mechanisms of MI have important implications for the use of MI in disciplines where PP is not possible, such as neurorehabilitation following brain injury (e.g., stroke). Recently, MI has been targeted as an effective tool for rehabilitation after stroke, as it is a clinically feasible method to drive brain activation in regions necessary for recovery to occur (Johansson, 2011; Hovington and Brouwer, 2010; Barclay-Goddard et al., 2011; MacIntyre et al., 2018), even in the absence of the ability for physical execution. Yet, despite the seemingly sound physiological basis for its efficacy in facilitating functional recovery, contradictory findings have been reported in a number of recent systematic reviews and meta-analyses of randomized trials examining the efficacy of MI to drive upper limb recovery post-stroke (Barclay-Goddard et al., 2011; Ietswaart et al., 2011; Braun et al., 2013; Carrasco and Cantalapiedra, 2016; Machado et al., 2016). However, unlike physical therapies which are prescribed based on our substantial knowledge of its mechanisms as they relate to learning and recovery, derived from studies related to the evolution of learning in the brain, the same mechanisms have yet to be illuminated in MI. Collectively, the current work provides two key pieces of knowledge that may help inform on its use in rehabilitation: 1) that tasks employed in MI-based therapies should be tailored to an individual's prior experience (i.e., prior skill expertise), and 2) the application of MI in the early stages of skill (re)acquisition is supported, in that the current work provides evidence in support of the effectiveness of MI at the outset of learning and in scenarios when physical therapy is not be possible.

Firstly, tasks employed in clinical studies using MI typically involve simple movements and basic daily activities such as opening and closing of the hand, reaching towards household objects, or ironing (see Page et al., 2007; Ietswaart et al., 2011; Li et al., 2018 for examples). Despite being a core principle of repetitive task specific training that is the foundation of physical therapies, the use of salient, challenging, or client-driven tasks is typically not incorporated into MI-based interventions (Peters and Page, 2015). Critically, through demonstrating that novel tasks drive bilateral patterns of brain activity relative to tasks that the participant has expertise with (see Chapter 2), salient and challenging tasks would thus drive more focal patterns of activity in regions that may lead to improved recovery. Additionally, the greater reliance on posterior parietal regions during MI of novel tasks that we observed in Chapter 2 may further explain its limited efficacy in neurorehabilitation, as many parietal regions are commonly damaged post-stroke, yet damage to this area is most often not taken into account in clinical studies using MI. For instance, often only the hemisphere of the lesion is reported, and patients are not stratified into intervention groups or screened out from MI interventions based on lesion location (see Liu et al., 2004; Ietswaart et al., 2011; Page et al., 2011; de Vries et al., 2013 for examples). Indeed, our prior work and others has shown that inhibition to posterior parietal regions (induced through non-invasive brain stimulation) impairs MI performance and MI-based learning (Evans et al., 2016; Kraeutner et al., 2016a, 2019), and there is a growing body of evidence suggesting that damage resulting from stroke localized to parietal regions impairs MI ability (Sirigu et al., 1996; McInnes et al., 2016; Oostra et al., 2016).

Secondly, our findings suggest that MI is effective when applied in the early stages of skill acquisition or prior to PP – a finding that has important implications for when physical therapy is not possible. Further, in showing that MI was not effective following PP may indicate that the variability related to the way in which MI is applied in stroke (including the order in which bouts of MI is combined with PP in therapy, e.g., alternating with PP within a session or day, or alternating with PP across days) explains, at least in part, the inconsistencies of its effectiveness for neurorehabilitation noted in the literature. In studies examining the efficacy of MI for upper limb recovery post-stroke, there is a wide range of how MI is employed in the literature. For instance, Li et al. (2018) employed 45 min of MI training, five times a week for four weeks, following usual rehabilitation practices. In contrast, Liu et al. (2004) employed one-hour MI sessions, five days per week for three weeks, whereby patients performed three sets of daily tasks. However, alternating MI and physical task performance was included in the MI sessions such that patients could self-evaluate their errors during actual task performance. Additionally, Ietswaart et al. (2011) employed 45 mins of MI involving goal-directed movements of simple tasks and daily activities, action observation and visualization of objects and scenes, and mental rotation tasks of hands (i.e., ‘implicit’ imagery). As sessions were conducted three days per week over four weeks, in addition to the standard of care, MI was effectively alternating with PP-based therapies across days. Thus, the optimal parameters of MI-based training in stroke, including how to best combine MI with standard of care (e.g., prior to PP, alternating bouts of MI and PP) needs to be elucidated in future clinical studies.

5.6 CHALLENGES AND LIMITATIONS

5.6.1 Imagery ability

In the studies reported in this thesis, it is important to consider individual differences both in the strategy of imagery employed and imagery ability. Here, participants were instructed to perform kinaesthetic MI (i.e., from the first person perspective, focusing on the polysensory aspects of the movement; Stinear et al., 2006; Munzert and Zentgraf, 2009) delivered via an auditory script at the outset of the MI session (see Appendix D for the script used during the MI familiarization periods for the studies reported in Chapters 2-4), as this type of imagery is shown to recruit more regions from the motor network vs. visual imagery (i.e., from the third person perspective, focusing on the vividness of the picture). While we employed manipulation checks throughout our studies to assess the engagement and vividness of their MI performance, whether or not participants were imagining similar movements or movement components is unknown owing to the covert nature of MI. Further, the level of proficiency with which each movement was imagined remains a confound that is noteworthy to MI. Specifically, while a number of assessments of imagery ability have been previously established in the literature, these assessments primarily rely on participant self-report (for reviews see Holmes and Calmels, 2008; McAvinue and Robertson, 2008; Collet et al., 2011; Boe and Kraeutner, 2017; Cumming and Eaves, 2018). Here, we employed a well-established questionnaire (the MIQ-RS; Gregg et al., 2005; 2010; Butler et al., 2012), to all participants such that we could ensure a similar level of imagery ability across our groups for each of the studies (see Chapters 2-4). However, the range of scores on this questionnaire appears to be minimal within a population of healthy individuals. Specifically, we further assessed individual scores on the MIQ across a total of 132 healthy participants obtained from the studies reported in this thesis and in prior work (Kraeutner et al., 2018; 2019; see Appendix E). Only two participants overall were noted to report 'poor imagery ability' (i.e., as determined by an average score <42, whereby their average rating on each MIQ-RS item would be 3/7; Appendix E). Thus, here we suggest that participants may be over-rating their imagery ability due to a lack of familiarity with MI, or that these questionnaires lack the sensitivity to assess the specific components of imagery ability.

In particular, the ability to imagine a movement is comprised of the generation, maintenance, manipulation, and controllability of an image to achieve task goals/outcomes (Ptak et al., 2017; Cumming and Eaves, 2018; Eaves et al., 2018). As argued in Eaves et al. (2018), it is critical to capture individual differences at both the global and specific level of each of these components. In the current work, it remains unknown the extent to which individual differences in these components may have contributed to between-group results observed in Chapter 2 (athletes vs control) and how the neural representations of MI performance of a task may change over time due to improved imagery ability concurrent with MI-based practice (i.e., that imagery is a skill in itself). To provide preliminary insight on this elusive issue, we conducted an exploratory analysis on data reported within Chapter 2. Here, while our participants demonstrated high imagery ability as measured by the MIQ-RS (Gregg et al., 2005; 2010; Butler et al., 2012), participants in this study reported a range of their frequency of imagery-use (i.e., the extent to which they incorporated mental practice related to sport in their daily lives). While this measure does not specifically probe the frequency in which MI is employed to learn skills, it is possible that regularly engaging in any number of mental practice techniques captured by the questionnaire (e.g., meditation, non-motoric visualization, auditory imagery, goal setting, etc.) may impact the development of MI ability. Here, we generated a map of regions where frequency of use is correlated with beamformer pseudo-Z scores, thus reflecting a change in beta power, obtained across all participants, for the task which all participants had prior experience with (teeth-brushing). A higher frequency was thus correlated to greater changes in beta power. In contrast to expertise, which was shown to modulate brain activation primarily localized to regions that encompassed bilateral parietal regions, SMA, and contralateral precentral regions (see Chapter 2), frequency of imagery use linked to brain activation localized entirely to the ipsilateral hemisphere, encompassing primarily occipital regions, as well as ipsilateral precentral and postcentral gyrus (Appendix F). These ipsilateral occipital regions are linked to imagery vividness (Oostra et al., 2016), and are also shown to be consistently active during action observation (i.e., which relies heavily on bilateral occipital and parietal regions; Hardwick et al., 2018). In light of the current findings, the ease in which the individual is able to generate the motor image – either a kinaesthetic representation or an image of the familiarization video depicting the task (often employed in studies of MI, and as employed in all work reported in Chapters 2-4) – is likely developed coincidentally with task-specific MI-based practice. Yet, how imagery ability may develop distinctively from task-specific MI-based practice remains unknown in the literature, and future work is required to probe the way in which imagery ability is represented in MI-related patterns of brain activation.

5.6.2 Sample size

It is important to note the sample size of studies reported in Chapters 3 and 4, particularly in that a final *n* of 11/group was included our neuroimaging analyses. Beyond within-group differences observed in our behavioural measures, we observed a limited number of within-group differences in our neuroimaging analyses that reached statistical significance. A larger sample to increase power may result in the ability to capture marginal changes in within-group analyses that were undetected by the current analysis. Additionally, we employed fMRI as our neuroimaging modality in these chapters and consequently, limitations associated with BOLD should be taken into consideration. Critically, BOLD indirectly reflects an increased use of neural substrates and is limited by its low temporal resolution and ability to measure direct electrophysiological activity (Sutton et al., 2009). While a wealth of literature has reported the upregulation of neuronal activity, localized to a network comprising of mainly frontal and parietal areas and core motor areas (Hétu et al., 2013; Hardwick et al., 2018), the extent to which neuronal upregulation occurs is less than that observed during PP of the same task (as evidenced from investigations comparing MI and PP of the same task employing direct electrophysiological measures; Burianová et al., 2013; Kraeutner et al., 2014; Duann and Chiou, 2016)). Further, as many complex tasks cannot be performed in a scanner, the body of knowledge comparing brain activation between MI and PP stems primarily from simple tasks that lack generalizability (Wulf and Shea, 2002). Thus, it is unknown how the extent to which neuronal upregulation during MI relative to PP may be further modulated by task complexity.

Moreover, in the studies reported in Chapters 3 and 4, the duration of each imagery block during the functional runs was ~30sec. We employed ~30sec blocks to mirror the time it took to perform the task both physically and through MI during each behavioural session (i.e., one block of dart throws during the behavioural sessions lasted ~30sec), and also typical of task-based fMRI designs to capture changes in hemodynamic response function. While we observed limited changes in MI-related activation within either of our groups following both the first and second half of training, greater activation was observed overall (i.e., post-training scan > pre-training scan, regardless of the order of practice modality; MI-PP or PP-MI), localized primarily to bilateral parietal-occipital regions encompassing the cuneus, precuneus, inferior and superior occipital gyri, and fusiform gyri. As outlined in Chapter 4, it is likely that these training-related changes reflect greater visual control and perceptual learning (Gauthier et al., 2000; Milton et al., 2007; Kim et al., 2008), indicative of more robust effector independent representation of the skill during MI. In contrast to studies employing fMRI, neuroimaging work employing MEG allow for electrophysiological activity to be directly assessed on a trial-by-trial basis, as activity is captured on the order of msec. Work assessing brain activation during MI typically employ analyses that focused on a <10 sec window following the 'go' cue based on observed MI-related changes in ERD (for examples see Kraeutner et al., 2014; Solomon et al., 2019; Chapter 2). Critically, prior work also shows that the period for which brain activity during MI is sustained is notably shorter relative to PP (Burianová et al., 2013; Kraeutner et al., 2014; Duann and Chiou, 2016). Thus, it is possible that any lasting changes in the MI-related brain activation driven by training within-groups in the studies reported in Chapters 3 and 4 may be too minimal or not sustained long enough to be observed via fMRI (Pfurtscheller and Neuper, 1997; Kraeutner et al., 2014). Taking the above together, a multi-modal approach is therefore necessary to address questions related to the neural underpinnings of MI.

5.6.3 Regional-based neuroimaging analyses

Methodological limitations associated with our regional-based approach in our neuroimaging analyses should also be considered, as this approach may underscore nuances observed in our between-group comparisons noted in Chapter 2 (namely, that there were no between-group differences observed between the volleyball group and the recreational controls when controlling for task-expertise), and contribute to the limited number of within-group differences reported in Chapters 3 and 4 observed in our analyses that reached statistical significance. In particular, a source-level analysis was employed in Chapter 2 on data obtained via MEG to examine beta ERD, indicative of regional-based brain activation linked to motor planning, imagery, and execution. In Chapters 3 and 4, we generated activation maps to elucidate spatial patterns of brain activation obtained through fMRI. However, these analyses do not permit the extent to which disparate regions are synchronous to be probed (termed functional connectivity; Sun et al., 2004; Schnitzler and Gross, 2005; Rubinov and Sporns, 2010; Brookes et al., 2011). While functional connectivity analyses have advanced our understanding of skill acquisition achieved through physical practice (i.e., in addition to examining regional patterns of brain activation), little is known about network reorganization following MI-based practice.

Generally, motor skill acquisition via PP is characterised by an increase in connectivity in cortico-subcortical circuits, and within fronto-parietal circuits thought to reflect heightened reliance on cognitive resources in the early stages of learning (Sun et al., 2007; Hanakawa et al., 2008; Dayan and Cohen, 2011; Doyon et al., 2011; Lin et al., 2013). For instance, after five days of training on a key-press sequence task, Lin et al. (2013) demonstrated increased coupling between dLPFC, parietal cortices, and cerebellum, as well as between the dLPFC and the caudate nucleus. The increased connectivity observed between dLPFC and fronto-parietal areas was linked to greater efficiency in retrieval processes (or executive functioning required to successfully access sequence representations). Further, increased connectivity observed between prefrontal and subcortical areas was linked to skill automaticity. Thus, as activation within specific regions may not change throughout practice, how their interactions evolve is important to understanding plasticity associated with skilled performance (Kelly and Garavan, 2005; Debarnot et al., 2014).

Interestingly, findings of the present work indicate that encoding facilitated through MI is central to the early stages of skill acquisition and the cerebellar-based system is not relied on for error detection/correction (see Chapter 4). Given the greater reliance on cognitive processes during early stages of skill acquisition, reflected through greater connectivity between premotor and prefrontal areas during these early stages (Petersen et al., 1998; Hikosaka et al., 2002; Sun et al., 2007), it is reasonable to hypothesize that connectivity between these regions would be heightened in MI vs. PP at the outset of learning. Indeed, Zhang et al., (2012) observed a decrease in coupling between posterior parietal and cortical regions following 14 days of MI-based training on a key-press sequence task, likely reflecting heightened efficiency of effector independent encoding or accessing the effector independent representations following MI-based practice. Notably, Xu et al (2014) sought to determine the key ‘node’ of information transfer (i.e., the region with the greatest number of connections to disparate regions, highlighting a region central to controlling information flow within a network; Reijneveld et al., 2007; Rubinov and Sporns, 2010) within the MI network relative to PP. In contrast to PP, in which the key node was determined to be the SMA, the key node in MI was localized to the premotor cortex during the same (key-press) task (Xu et al., 2014). Taking this work together, while similar substrates underlie the MI and PP networks, the flow of information transfer may occur in a different manner, further evidenced by a difference in functional reorganization of the motor network following MI- vs. PP-based training. Thus, as characterising changes in network connectivity may provide a more nuanced investigation into the mechanisms underlying MI, the identification of key nodes, and probing the strength and direction of information transfer between nodes (Reijneveld et al., 2007; Rubinov and Sporns, 2010) over the course of MI-based training represents an important next step in the literature.

5.7 CONCLUSION

Building on prior theories of MI, how the nature of MI differs from PP, owing to the lack of sensory feedback during this modality of practice, has emerged as a critical gap in our understanding of MI. Here it is shown that while MI shares neural substrates and representations of skill expertise with PP, its nature as a modality of skill acquisition is fundamentally different as different information is encoded during MI relative to PP. Namely, MI drives encoding of effector independent representations that manifest as improvements in global aspects of performance, yet alterations to the motor program are less robust in MI as these representations are not mapped to specific effectors. Thus, despite being considered analogous to PP, findings from the current work provide insight as to why improvements in performance driven via MI remain inferior to those driven by PP. Stemming from the current work, a critical line of questioning pertaining to the specific processes that underlie error detection and correction in MI has emerged. Critically, the present work has important implications for how the mechanisms of MI are probed. In particular, novelty associated with the skill being performed in neuroimaging studies (through MI or PP) should be taken into consideration when evaluating resultant patterns of brain activation. Further, the present work highlights the need to increase the resolution of outcome measures probing training-related effects driven through MI. Namely, that future studies examining the effects of MI-based practice should consider the use of transfer tasks to directly probe effector independent encoding (i.e., vs. strictly effector dependent encoding). Collectively, this work represents an important step forward in understanding the nature of MI as a modality of skill acquisition.

5.8 REFERENCES

Amemiya K, Ishizu T, Ayabe T, Kojima S (2010) Effects of motor imagery on intermanual transfer: a near-infrared spectroscopy and behavioural study. Brain research 1343:93–103.

Baeck J-SS, Kim Y-TT, Seo J-HH, Ryeom H-KK, Lee J, Choi S-MM, Woo M, Kim W, Kim JG, Chang Y (2012) Brain activation patterns of motor imagery reflect plastic changes associated with intensive shooting training. Behav Brain Res 234:26–32.

Bar RJ, DeSouza JF (2016) Tracking Plasticity: Effects of Long-Term Rehearsal in Expert Dancers Encoding Music to Movement. PLoS ONE 11:e0147731.

Barclay-Goddard RE, Stevenson TJ, Poluha W, Thalman L (2011) Mental practice for treating upper extremity deficits in individuals with hemiparesis after stroke. Cochrane Database Syst Rev:CD005950.

Binkofski F, Buxbaum LJ (2013) Two action systems in the human brain. Brain Lang 127:222–229.

Boe S, Gionfriddo A, Kraeutner S, Tremblay A, Little G, Bardouille T (2014) Laterality of brain activity during motor imagery is modulated by the provision of source level neurofeedback. Neuroimage 101:159–167.

Boe S, Kraeutner S (2017) Assessing Motor Imagery Ability Through Imagery-Based Learning: An Overview and Introduction to Miscreen, a Mobile App for Imagery Assessment. Imagination Cognition Personality:027623661773504.

Braun S, Kleynen M, van Heel T, Kruithof N, Wade D, Beurskens A (2013) The effects of mental practice in neurological rehabilitation; a systematic review and meta-analysis. Front Hum Neurosci 7:390.

Brookes MJ, Hale JR, Zumer JM, Stevenson CM, Francis ST, Barnes GR, Owen JP, Morris PG, Nagarajan SS (2011) Measuring functional connectivity using MEG: methodology and comparison with fcMRI. Neuroimage 56:1082–1104.

Burianová H, Marstaller L, Sowman P, Tesan G, Rich A, Williams M, Savage G, Johnson B (2013) Multimodal functional imaging of motor imagery using a novel paradigm. NeuroImage 71:50–58.

Buxbaum LJ, Kyle K, Grossman M, Coslett HB (2007) Left inferior parietal representations for skilled hand-object interactions: evidence from stroke and corticobasal degeneration. Cortex 43:411–423.

Buxbaum LJ, Kyle KM, Menon R (2005) On beyond mirror neurons: internal representations subserving imitation and recognition of skilled object-related actions in humans. Brain Res Cogn Brain Res 25:226–239.

Buxbaum LJ, Kyle KM, Tang K, Detre JA (2006) Neural substrates of knowledge of hand postures for object grasping and functional object use: evidence from fMRI. Brain Res 1117:175–185.

Carrasco G, Cantalapiedra A (2016) Effectiveness of motor imagery or mental practice in functional recovery after stroke: a systematic review. Neurología (English Edition) 31(1):43-52.

Chang Y, Lee J-J, Seo J-H, Song H-J, Kim Y-T, Lee H, Kim H, Lee J, Kim W, Woo M, Kim J (2010) Neural correlates of motor imagery for elite archers. NMR in Biomedicine 24:366-72.

Collet C, Guillot A, Lebon F, MacIntyre T, Moran A (2011) Measuring motor imagery using psychometric, behavioral, and psychophysiological tools. Exerc Sport Sci Rev 39:85–92.

Cumming J, Eaves DL (2018) The Nature, Measurement, and Development of Imagery Ability. Imagination, Cognition and Personality 37:375–393.

Dahm S, Rieger M (2019) Is imagery better than reality? Performance in imagined dart throwing. Hum Movement Sci 66:38–52.

Dayan E, Cohen LG (2011) Neuroplasticity subserving motor skill learning. Neuron 72:443–454.

De Vries S, Tepper M, Feenstra W, Oosterveld H, Boonstra AM, Otten B (2013) Motor imagery ability in stroke patients: the relationship between implicit and explicit motor imagery measures. Front Hum Neurosci 7:790.

Debarnot U, Sperduti M, Di Rienzo F, Guillot A (2014) Experts bodies, experts minds: How physical and mental training shape the brain. Front Hum Neurosci 8:280.

Del Percio C, Infarinato F, Iacoboni M, Marzano N, Soricelli A, Aschieri P, Eusebi F, Babiloni C (2010) Movement-related desynchronization of alpha rhythms is lower in athletes than non-athletes: a high-resolution EEG study. Clin Neurophysiol 121:482–491.

Di Rienzo F, Debarnot U, Daligault S, Saruco E, Delpuech C, Doyon J, Collet C, Guillot A (2016) Online and Offline Performance Gains Following Motor Imagery Practice: A Comprehensive Review of Behavioral and Neuroimaging Studies. Front Hum Neurosci 10:315.

Doyon J, Orban P, Barakat M, Debas K, Lungu O, Albouy G, Fogel S, Proulx S, Laventure S, Deslauriers J, Duchesne C, Carrier J, Benali H (2011) Functional brain plasticity associated with motor learning. Med Sci (Paris) 27:413–420.

Duann J-RR, Chiou J-CC (2016) A Comparison of Independent Event-Related Desynchronization Responses in Motor-Related Brain Areas to Movement Execution, Movement Imagery, and Movement Observation. PLoS ONE 11:e0162546.

Eaves DL, Emerson JR, Binks JA, Scott MW, Kenny RPWP (2018) Imagery ability: the individual difference gradient and novel training methods (Commentary on Kraeutner et al. (2018)). Eur J Neurosci 47:1219–1220.

Evans C, Edwards MG, Taylor LJ, Ietswaart M (2016) Perceptual decisions regarding object manipulation are selectively impaired in apraxia or when tDCS is applied over the left IPL. Neuropsychologia 86:153–166.

Frank C, Land WM, Schack T (2015) Perceptual-Cognitive Changes During Motor Learning: The Influence of Mental and Physical Practice on Mental Representation, Gaze Behavior, and Performance of a Complex Action. Front Psychol 6:1981.

Frank C, Schack T (2017) The Representation of Motor (Inter)action, States of Action, and Learning: Three Perspectives on Motor Learning by Way of Imagery and Execution. Front Psychol 8:678.

Gauthier I, Skudlarski P, Gore JC, Anderson AW (2000) Expertise for cars and birds recruits brain areas involved in face recognition. Nat Neurosci 3:191–197.

Guo Z, Li A, Yu L (2017) "Neural Efficiency" of Athletes' Brain during Visuo-Spatial Task: An fMRI Study on Table Tennis Players. Front Behav Neurosci 11:72.

Hanakawa T, Dimyan M, Hallett M (2008) Motor Planning, Imagery, and Execution in the Distributed Motor Network: A Time-Course Study with Functional MRI. Cerebral Cortex 18:2775–2788.

Hardwick RM, Caspers S, Eickhoff SB, Swinnen SP (2018) Neural correlates of action: Comparing meta-analyses of imagery, observation, and execution. Neurosci Biobehav Rev 94:31–44.

Haufler AJ, Spalding TW, Santa Maria DL, Hatfield BD (2000) Neuro-cognitive activity during a self-paced visuospatial task: comparative EEG profiles in marksmen and novice shooters. Biol Psychol 53:131–160.

Hayes S, Ryan L, Schnyer D, Nadel L (2004) An fMRI Study of Episodic Memory: Retrieval of Object, Spatial, and Temporal Information. Behav Neurosci 118:885.

Hétu S, Grégoire M, Saimpont A, Coll M-P, Eugène F, Michon P-E, Jackson P (2013) The neural network of motor imagery: An ALE meta-analysis. Neuroscience and biobehavioral reviews 37:930–949.

Hikosaka O, Nakamura K, Sakai K, Nakahara H (2002) Central mechanisms of motor skill learning. Curr Opin Neurobiol 12:217–222.

Holmes P, Calmels C (2008) A neuroscientific review of imagery and observation use in sport. J Mot Behav 40:433–445.

Holmes P, Collins D (2001) The PETTLEP Approach to Motor Imagery: A Functional Equivalence Model for Sport Psychologists. J Appl Sport Psychol 13:60–83.

Hovington C, Brouwer B (2010) Guided motor imagery in healthy adults and stroke: does strategy matter? Neurorehabilitation and neural repair 24:851–857.

Ietswaart M, Johnston M, Dijkerman HC, Joice S, Scott CL, MacWalter RS, Hamilton SJ (2011) Mental practice with motor imagery in stroke recovery: randomized controlled trial of efficacy. Brain 134:1373–1386.

Ingram TG, Kraeutner SN, Solomon JP, Westwood DA, Boe SG (2016) Skill acquisition via motor imagery relies on both motor and perceptual learning. Behav Neurosci 130:252–260.

Ingram TGJG, Solomon JP, Westwood DA, Boe SG (2019) Movement related sensory feedback is not necessary for learning to execute a motor skill. Behav Brain Res 359:135–142.

Jeannerod M (2001) Neural Simulation of Action: A Unifying Mechanism for Motor Cognition. NeuroImage 14:S103–S109.

Johansson B (2011) Current trends in stroke rehabilitation. A review with focus on brain plasticity: Stroke rehabilitation. Acta Neurologica Scandinavica 123:147–159.

Kelly AM, Garavan H (2005) Human functional neuroimaging of brain changes associated with practice. Cereb Cortex 15:1089–1102.

Kilteni K, Andersson BJ, Houborg C, Ehrsson HH (2018) Motor imagery involves predicting the sensory consequences of the imagined movement. Nat Commun 9:187.

Kim J, Lee H, Kim W, Park H, Kim S, Moon D, Woo M, Tennant L (2008) Neural correlates of pre-performance routines in expert and novice archers. Neurosci Lett 445:236–241.

Kim T, Frank C, Schack T (2017) A Systematic Investigation of the Effect of Action Observation Training and Motor Imagery Training on the Development of Mental Representation Structure and Skill Performance. Front Hum Neurosci 11:499.

Kohl R, Roenker D (1980) Bilateral Transfer as a Function of Mental Imagery. J Motor Behav 12:197–206.

Kohl RM, Roenker DL (1983) Mechanism involvement during skill imagery. J Mot Behav 15:179–190.

Kraeutner S, Gionfriddo A, Bardouille T, Boe S (2014) Motor imagery-based brain activity parallels that of motor execution: Evidence from magnetic source imaging of cortical oscillations. Brain research 1588:81–91.

Kraeutner SN, El-Serafi M, Lee J, Boe SG (2019) Disruption of motor imagery performance following inhibition of the left inferior parietal lobe. Neuropsychologia 127:106-112.

Kraeutner SN, Gaughan TC, Eppler SN, Boe SG (2017) Motor imagery-based implicit sequence learning depends on the formation of stimulus response associations. Acta Pscyhologica 31:48–55.

Kraeutner SN, Keeler LT, Boe SG (2016a) Motor imagery-based skill acquisition disrupted following rTMS of the inferior parietal lobule. Experimental brain research 234:397–407.

Kraeutner SN, MacKenzie LA, Westwood DA, Boe SG (2016b) Characterizing skill acquisition through motor imagery with no prior physical practice. Journal of experimental psychology Human perception and performance 42:257–265.

Lacourse MG, Orr EL, Cramer SC, Cohen MJ (2005) Brain activation during execution and motor imagery of novel and skilled sequential hand movements. Neuroimage 27:505–519.

Lacourse MG, Turner JA, Randolph-Orr E, Schandler SL, Cohen MJ (2004) Cerebral and cerebellar sensorimotor plasticity following motor imagery-based mental practice of a sequential movement. J Rehabil Res Dev 41:505–524.

Lafleur MF, Jackson PL, Malouin F, Richards CL, Evans AC, Doyon J (2002) Motor learning produces parallel dynamic functional changes during the execution and imagination of sequential foot movements. Neuroimage 16:142–157.

Land WM, Liu B, Cordova A, Fang M, Huang Y, Yao WX (2016) Effects of Physical Practice and Imagery Practice on Bilateral Transfer in Learning a Sequential Tapping Task. PLoS ONE 11:e0152228.

Lee TD (1988) Transfer-Appropriate Processing: A Framework for Conceptualizing Practice Effects in Motor Learning. Advances in Psychology 50:201–215.

Li F, Zhang T, Li B-J, Zhang W, Zhao J, Song L-P (2018) Motor imagery training induces changes in brain neural networks in stroke patients. Neural Regen Res 13:1771–1781.

Lin C, Chiang M, Knowlton B, Iacoboni M, Udompholkul P, Wu A (2013) Interleaved practice enhances skill learning and the functional connectivity of fronto-parietal networks. Human Brain Mapping 34:1542–1558.

Liu KP, Chan CC, Lee TM, Hui-Chan CW (2004) Mental imagery for promoting relearning for people after stroke: a randomized controlled trial. Arch Phys Med Rehabil 85:1403–1408.

Lohse K, Healy A, Sherwood D (2010) Mental Practice in the Intermanual Transfer of Motor Skills. J Imag Res Sport Phys Activity 5:6.

Machado S, Lattari E, Paes F, Rocha NB, Nardi AE, Arias-Carrión O, Mura G, Yuan T-FF, Carta MG, Campos C (2016) Mental Practice Combined with Motor Rehabilitation to Treat Upper Limb Hemiparesis of Post-Stroke Patients: Clinical and Experimental Evidence. Clin Pract Epidemiol Ment Health 12:9–13.

MacIntyre T, Madan C, Moran A, Collet C, Guillot A (2018) Motor imagery, performance and motor rehabilitation. Progress In Brain Research 240:141-159.

McAvinue L, Robertson I (2008) Measuring motor imagery ability: A review. Eur J Cogn Psychol 20:232–251.

McInnes K, Friesen C, Boe S (2016) Specific Brain Lesions Impair Explicit Motor Imagery Ability: A Systematic Review of the Evidence. Arch Phys Med Rehabil 97:478–489.e1.

Milton J, Small SL, Solodkin A (2008) Imaging motor imagery: methodological issues related to expertise. Methods 45:336–341.

Milton J, Solodkin A, Hluatík P, Small S (2007) The mind of expert motor performance is cool and focused. NeuroImage 35:804–813.

Munzert J, Zentgraf K (2009) Motor imagery and its implications for understanding the motor system. Progress in Brain Research 174:219–229.

Nyberg L, Eriksson J, Larsson A, Marklund P (2006) Learning by doing versus learning by thinking: An fMRI study of motor and mental training. Neuropsychologia 44:711–717.

Nyberg L, McIntosh AR, Cabeza R, Habib R, Houle S, Tulving E (1996) General and specific brain regions involved in encoding and retrieval of events: what, where, and when. Proc Natl Acad Sci USA 93:11280–11285.

O’Shea H, Moran A (2017) Does Motor Simulation Theory Explain the Cognitive Mechanisms Underlying Motor Imagery? A Critical Review. Front Hum Neurosci 11:72.

Olsson C-J, Jonsson B, Nyberg L (2008) Learning by doing and learning by thinking: an fMRI study of combining motor and mental training. Frontiers in Human Neuroscience 2:5.

Ono T, Kimura A, Ushiba J (2013) Daily training with realistic visual feedback improves reproducibility of event-related desynchronisation following hand motor imagery. Clinical Neurophysiology 124:1779–1786.

Oostra KM, Van Bladel A, Vanhoonacker AC, Vingerhoets G (2016) Damage to Fronto-Parietal Networks Impairs Motor Imagery Ability after Stroke: A Voxel-Based Lesion Symptom Mapping Study. Front Behav Neurosci 10:5.

Page SJ, Dunning K, Hermann V, Leonard A, Levine P (2011) Longer versus shorter mental practice sessions for affected upper extremity movement after stroke: a randomized controlled trial. Clin Rehabil 25:627–637.

Page SJ, Levine P, Leonard A (2007) Mental practice in chronic stroke: results of a randomized, placebo-controlled trial. Stroke 38:1293–1297.

Percio C, Rossini P, Marzano N, Iacoboni M, Infarinato F, Aschieri P, Lino A, Fiore A, Toran G, Babiloni C, Eusebi F (2008) Is there a “neural efficiency” in athletes? A high-resolution EEG study. Neuroimage 42:1544–1553.

Peters HT, Page SJ (2015) Integrating Mental Practice with Task-specific Training and Behavioral Supports in Poststroke Rehabilitation: Evidence, Components, and Augmentative Opportunities. Phys Med Rehabil Clin N Am 26:715–727.

Petersen S, Mier H, Fiez J, Raichle M (1998) The effects of practice on the functional anatomy of task performance. Proc National Acad Sci 95:853–860.

Pfurtscheller G, Neuper C (1997) Motor imagery activates primary sensorimotor area in humans. Neuroscience Letters 239:6568.

Ptak R, Schnider A, Fellrath J (2017) The Dorsal Frontoparietal Network: A Core System for Emulated Action. Trends Cogn Sci (Regul Ed) 21:589–599.

Rieger M, Massen C (2014) Tool characteristics in imagery of tool actions. Psychological Res 78:10–17.

Rienhoff R, Hopwood MJ, Fischer L, Strauss B, Baker J, Schorer J (2013) Transfer of motor and perceptual skills from basketball to darts. Front Psychol 4:593.

Rizzolatti G, Cattaneo L, Fabbri-Destro M, Rozzi S (2014) Cortical mechanisms underlying the organization of goal-directed actions and mirror neuron-based action understanding. Physiol Rev 94:655–706.

Rizzolatti G, Matelli M (2003) Two different streams form the dorsal visual system: anatomy and functions. Experimental Brain Research 153:146–157.

Ross J, Tkach J, Ruggieri P, Lieber M, Lapresto E (2003) The mind s eye: functional MR imaging evaluation of golf motor imagery. American Journal of Neuroradiology 24:1036 1044.

Rubinov M, Sporns O (2010) Complex network measures of brain connectivity: uses and interpretations. Neuroimage 52:1059–1069.

Schnitzler A, Gross J (2005) Functional connectivity analysis in magnetoencephalography. Int Rev Neurobiol 68:173–195.

Sirigu A, Duhamel JR, Cohen L, Pillon B, Dubois B, Agid Y (1996) The mental representation of hand movements after parietal cortex damage. Science 273:1564–1568.

Smith D, Wright CJ, Cantwell C (2008) Beating the bunker: the effect of PETTLEP imagery on golf bunker shot performance. Res Q Exerc Sport 79:385–391.

Solodkin A (2004) Fine Modulation in Network Activation during Motor Execution and Motor Imagery. Cerebral Cortex 14:1246–1255.

Solomon JP, Kraeutner SN, Bardouille T, Boe SG (*under review - BRES-D-18-01445_R2*) Probing the temporal dynamics of movement inhibition in motor imagery.

Stinear C, Byblow W, Steyvers M, Levin O, Swinnen S (2006) Kinesthetic, but not visual, motor imagery modulates corticomotor excitability. Experimental Brain Research 168:157–164.

Sun F, Miller L, D'Esposito M (2004) Measuring interregional functional connectivity using coherence and partial coherence analyses of fMRI data. NeuroImage 21:647–658.

Sun FT, Miller LM, Rao AA, D'Esposito M (2007) Functional connectivity of cortical networks involved in bimanual motor sequence learning. Cereb Cortex 17:1227–1234.

Sutton B, Ouyang C, Karampinos D, Miller G (2009) Current trends and challenges in MRI acquisitions to investigate brain function. International Journal of Psychophysiology 73:33–42.

Tian X, Poeppel D (2010) Mental imagery of speech and movement implicates the dynamics of internal forward models. Auditory Cognitive Neurosci 1:166.

Vickers J (1996) Visual control when aiming at a far target. J Exp Psychology Hum Percept Perform 22:342.

Wohldmann EL, Healy AF, Lyle BEJ (2007) Pushing the limits of imagination: Mental practice for learning sequences. Journal of Experimental Psychology: Learning, Memory, and Cognition 33:254261.

Woodworth RS, Thorndike EL (1901) The influence of improvement in one mental function upon the efficiency of other functions. (I). Psychological Review 8:247–261.

Wulf G, Shea CH (2002) Principles derived from the study of simple skills do not generalize to complex skill learning. Psychonomic bulletin & review 9(2):185-211.

Xu L, Zhang H, Hui M, Long Z, Jin Z, Liu Y, Yao L (2014) Motor execution and motor imagery: a comparison of functional connectivity patterns based on graph theory. Neuroscience 261:184–194.

Yang J (2015) The influence of motor expertise on the brain activity of motor task performance: A meta-analysis of functional magnetic resonance imaging studies. Cognitive Affect Behav Neurosci 15:381–394.

Yarrow K, Brown P, Krakauer JW (2009) Inside the brain of an elite athlete: the neural processes that support high achievement in sports. Nat Rev Neurosci 10:585–596.

Zentgraf K, Green N, Munzert J, Schack T, Tenenbaum G, Vickers JN, Weigelt M, Wolfensteller U, Heekeren HR (2009) How are actions physically implemented? Prog Brain Res 174:303–318.

Zhang H, Xu L, Zhang R, Hui M, Long Z, Zhao X, Yao L (2012) Parallel Alterations of Functional Connectivity during Execution and Imagination after Motor Imagery Learning. PLoS ONE 7:e36052.

Zhang Q, Zhang P, Song L, Yang Y, Yuan S, Chen Y, Sun S, Bai X (2019) Brain Activation of Elite Race Walkers in Action Observation, Motor Imagery, and Motor Execution Tasks: A Pilot Study. Front Hum Neurosci 13:80.

Zhang T, Liu T, Li F, Li M, Liu D, Zhang R, He H, Li P, Gong J, Luo C, Yao D, Xu P (2016) Structural and functional correlates of motor imagery BCI performance: Insights from the patterns of fronto-parietal attention network. Neuroimage 134:475–485.

Appendix A: Supplementary Materials for Chapter 2

As described in the general discussion and further below, various supplementary analyses were conducted on data collected over the course of this dissertation.

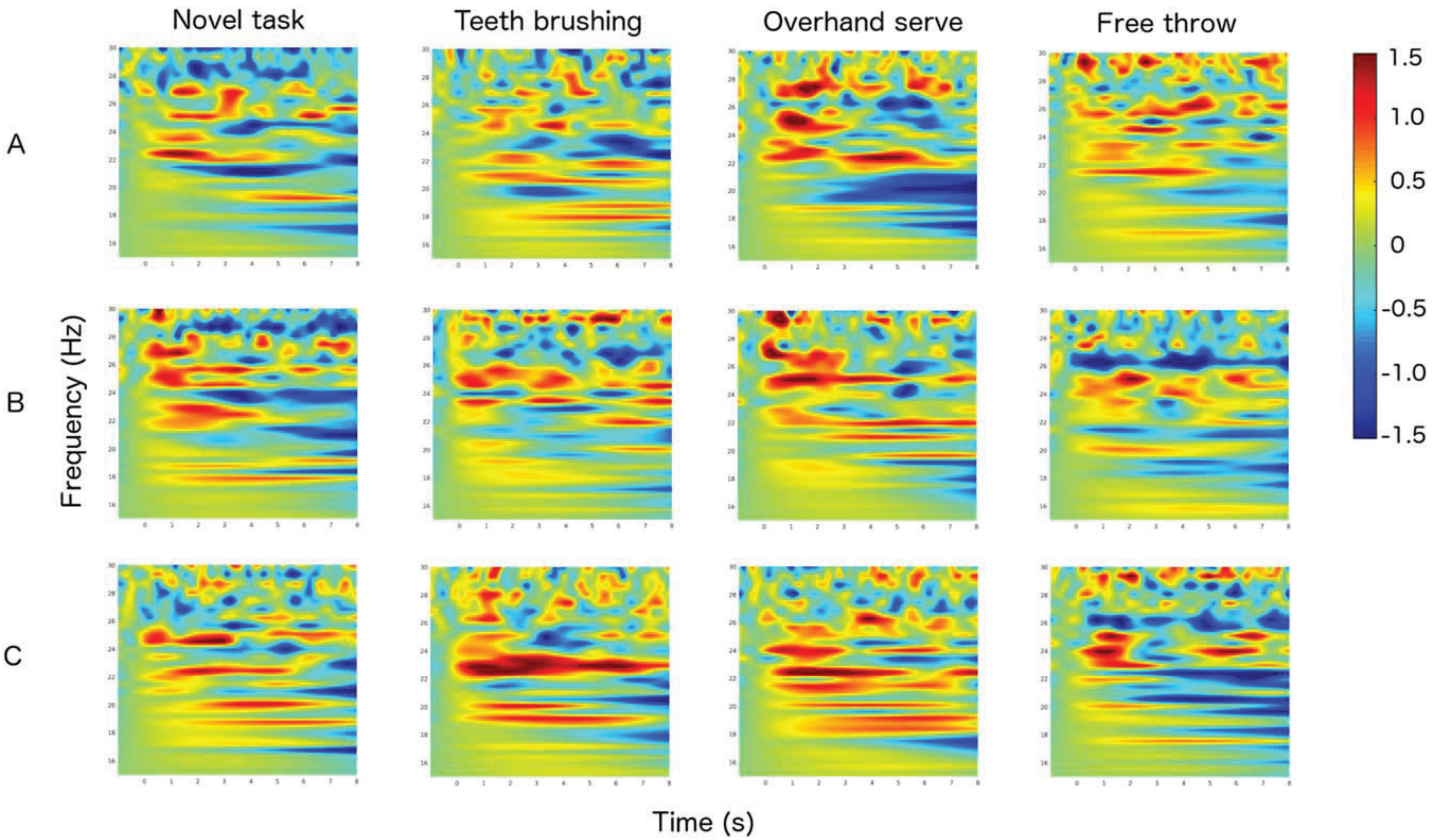


Figure 6.1 Time-frequency response plots for the beta (15-30 Hz) frequency band averaged across 50 MEG sensors (centred on the midline and encompassing bilateral sensorimotor regions), for each task across for the basketball (A), volleyball (B), and control group (C). A Morlet wavelet analysis (128 samples and 32 frequency bins) was applied after parsing each trial with an interval of 2 sec prior to and 9 sec following the "Go" cue

(time = 0). The first and last seconds of data were cropped to remove edge effects due to the wavelet transformation, and time-frequency responses were then normalized to the baseline interval (2 sec prior to the “Go” cue). Finally TFRs were averaged at a group level for each task condition.

Appendix B: MI-related activation

Table 6.1

MNI coordinates of local maxima resulting from the task-positive network (MI vs. rest) across all participants at the pre-training scan.

Anatomical region	MNI coordinates			Z-score
	x	y	z	
Pre-training scan				
L Inferior frontal gyrus (orbital)	-39	38	-15	5.49
L Inferior frontal gyrus (orbital)	-45	43	-6	5.39
L Inferior frontal gyrus (orbital)	-47	43	-6	5.37
L Precentral gyrus	-26	-15	73	5.35
R Superior temporal gyrus	53	-8	1	5.48
R Inferior frontal gyrus (orbital)	38	42	-11	5.3
R Cerebellum	16	-65	-59	5.46
R Cerebellum	10	-68	-59	5.04
R Cerebellum	12	-67	-59	4.89
R Cerebellum	4	-70	-55	4.86
R Cerebellum	17	-61	-59	4.84

R Cerebellum	15	-58	-57	4.66
Mid-training scan				
L Insula	-45	-4	-2	6.23
L Superior temporal gyrus	-49	-12	2	6.18
L Superior temporal gyrus	-46	-2	-5	5.73
L Superior temporal gyrus	-43	-10	-5	5.67
R Insula	48	2	-5	6.19
R Insula	48	5	-5	6.12
Post-training scan				
R Insula	*45*	*8*	*-7*	5.89
R Superior temporal gyrus	*51*	*-1*	*-6*	5.9
R Superior temporal gyrus	*60*	*-24*	*7*	5.73
R Superior temporal gyrus	*62*	*-12*	*3*	5.61
R Superior temporal gyrus	*61*	*-9*	*3*	5.57
R Superior temporal pole	*48*	*8*	*-8*	5.63

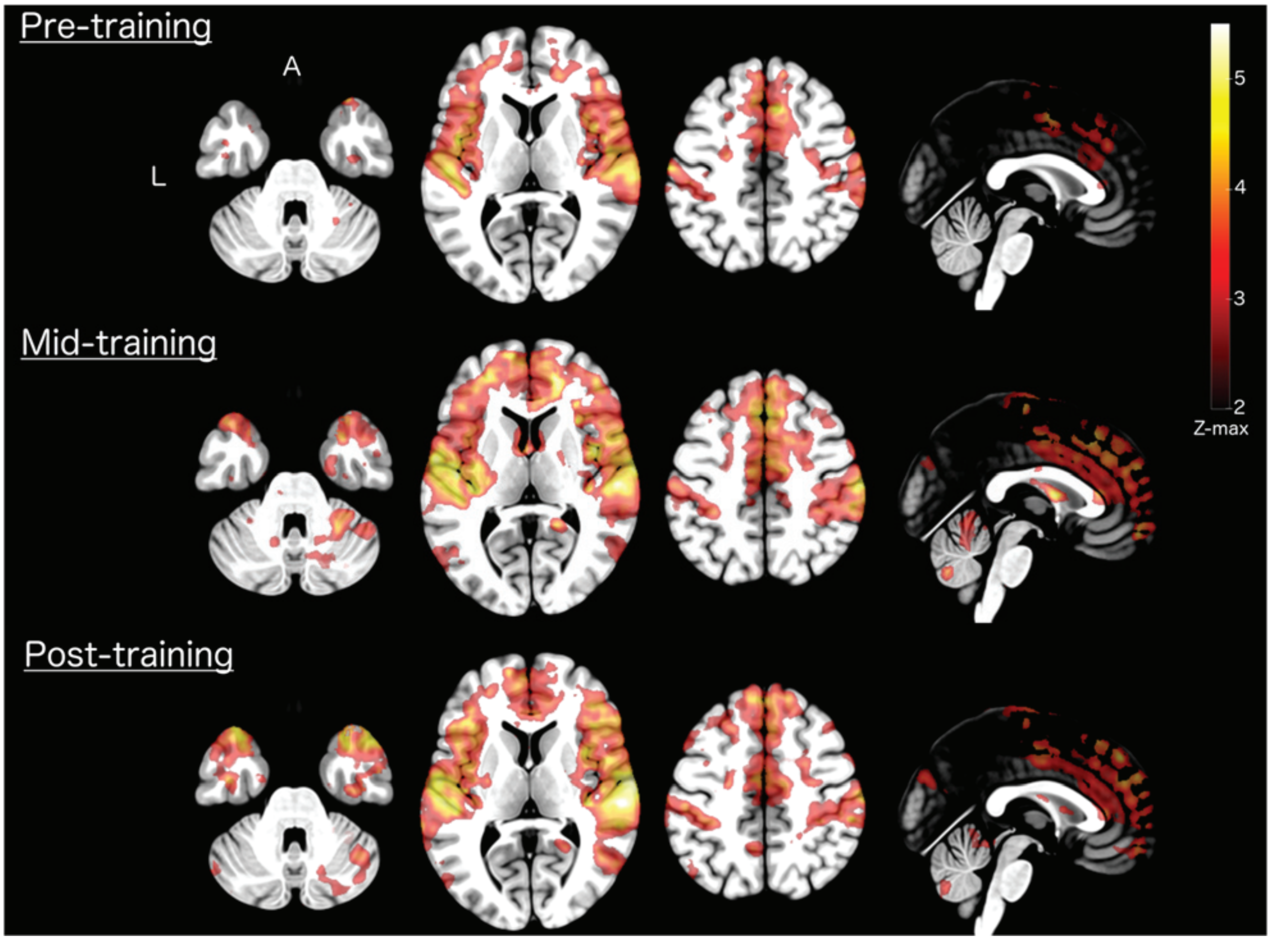


Figure 6.2 Motor imagery-based brain activity (MI vs. rest) across all participants, where the colourbar represents the Z-max value. Activation was localized to regions including bilateral frontal, contralateral precentral, and ipsilateral cerebellar regions. Clusters shown reached a cluster corrected threshold ($Z>2.0$; $p < 0.05$), family-wise error corrected for number of comparisons, and are shown overlaid on the MNI template.

Appendix B: Supplementary Materials for Chapter 4

ACF1 calculation:

Formally, the ACF1 in the X and Y planes are defined as follows:

$$ACF1_x = \frac{E\{x(n)x(n+1)\}}{E\{x(n)x(n)\}}$$

$$ACF1_y = \frac{E\{y(n)y(n+1)\}}{E\{y(n)y(n)\}}$$

Where $E\{\,\}$ is the Expectation operation and is computed over all $= 1 \ldots \infty$. Where, in this case, *n* is the throw number and, X and Y are assumed to be independent stationary, zero mean, Gaussian random variables with standard deviations:

$$\sigma_x^2 = E\{x(n)x(n)\}$$

$$\sigma_y^2 = E\{y(n)y(n)\}$$

$$\sigma_x^2 = \sigma_y^2 = \sigma^2$$

For dart throwing let $c_x(n)$ and $c_y(n)$ be the Correction Factor in each plane that a thrower applies between successive attempts to hit the Bull's Eye.

$$x(n+1) = c_x(n)x(n)$$

$$y(n+1) = c_y(n)y(n)$$

Assume that the Correction Factors are random variables and independent of the previous throw. That is, the Correction Factors are only based on the skill level of the dart thrower and do not depend on the previous throw. Also assume that the Correction Factors in the X and Y plane are independent random variables from the same distribution. Thus:

$$ACF1_x = \frac{E\{x(n)x(n)\}\,E\{c_x(n)\}}{E\{x(n)x(n)\}} = \frac{\sigma^2\,\mu_{cx}}{\sigma^2} = \mu_{cx}$$

$$ACF1_y = \frac{E\{y(n)y(n)\}\, E\{c_y(n)\}}{E\{y(n)y(n)\}} = \mu_{cy}$$

$$\mu_{cx} = \mu_{cx} = \mu_c$$

ACF1 therefore computes the mean Correction Factor in each plane. A mean of zero reflects no skill as the improvement between throws is on average zero. A nonzero mean indicates that some improvement occurs between throws and so the dart thrower has some level of skill.

For a finite population with $n = 1 \ldots N$ the true $ACF1$ can only be estimated. A first approximation is obtained using finite summations as:

$$\widetilde{ACF1}_x = \frac{\sum_{n=1}^{N-1} x(n)x(n+1)}{\sum_{n=1}^{N} x(n)x(n)} * \frac{N}{(N-1)}$$

$$\widetilde{ACF1}_y = \frac{\sum_{n=1}^{N-1} y(n)y(n+1)}{\sum_{n=1}^{N} y(n)y(n)} * \frac{N}{(N-1)}$$

with N being the total number of throws during a testing session and the scaling factor $\frac{N}{N-1}$ accounting for the differing number of terms in the numerator and denominator. Note also that it is assumed that $x(n)$ and $y(n)$ are stationary, in that skill acquisition does occur during a test block. Thus N must be small enough to avoid skill acquisition but must also be large enough to obtain useful estimates of μ_c. Here we set $N = 15$.

Because N is necessarily small the first approximation is subject to bias introduced by nonzero means in the small sample populations for $x(n), x(n+1, y(n)$ and $y(n+1)$. Hence in the X plane:

$$x(n)x(n+1) = (x_z(n) + \mu_x)(x_z(n+1) + \mu_{x1} = x_z(n)x_z(n+1) + \mu_x\mu_{x1}$$

Where $x_z(n), x_z(n+1)$ are now zero mean and $\mu_x,\ \mu_{x1}$ are the means of $x(n), x(n+1)$ respectively and are computed over the appropriate indices. Similarly:

$$x(n)x(n) = (x_z(n) + \mu_x)(x_z(n) + \mu_x) = x_z^2(n) + \mu_x^2$$

Leading to the improved estimates:

$$\widehat{ACF1}_x = \frac{\frac{1}{N-1}\sum_{n=1}^{N-1} x(n)x(n+1) - \mu_x\mu_{x1}}{\frac{1}{N-1}\sum_{n=1}^{N-1} x(n)x(n) - \mu_x^2}$$

$$\widehat{ACF1}_y = \frac{\frac{1}{N-1}\sum_{n=1}^{N-1} y(n)y(n+1) - \mu_y\mu_{y1}}{\frac{1}{N-1}\sum_{n=1}^{N-1} y(n)y(n) - \mu_y^2}$$

With:

$$\mu_x = \frac{1}{N-1}\sum_{n=1}^{N-1} x(n)$$

$$\mu_{x1} = \frac{1}{N-1}\sum_{n=1}^{N-1} x(n+1)$$

$$\mu_y = \frac{1}{N-1}\sum_{n=1}^{N-1} y(n)$$

$$\mu_{y1} = \frac{1}{N-1}\sum_{n=1}^{N-1} y(n+1)$$

Table 6.2

Means (and SDs) for all kinematic variables.

			Test session			
			Day 1	Day 5	Day 6	Day 10
Shoulder (°)	Take back	MI-PP	63.0 (4.4)	65.7 (3.3)	66.16 (4.43)	67.47 (3.19)
		PP-MI	68.0 (5.2)	70.8 (2.8)	70.37 (3.23)	72.17 (2.78)
		PP-only	60.37 (13.41)	68.90 (12.09)	71.34 (15.12)	71.75 (12.59)
	Release	MI-PP	80.4 (5.3)	80.8 (5.7)	83.61 (4.16)	86.93 (3.85)
		PP-MI	82.8 (4.5)	85.3 (3.9)	83.16 (3.61)	84.57 (3.84)
		PP-only	80.54 (6.30)	84.45 (8.93)	85.08 (9.49)	84.72 (1.00)
Elbow (°)	Take back	MI-PP	36.2 (2.6)	36.9 (2.8)	37.30 (2.69)	37.11 (2.45)
		PP-MI	35.5 (3.1)	38.0 (2.7)	37.64 (2.77)	37.58 (2.34)
		PP-only	35.54 (5.68)	40.96 (9.54)	41.21 (9.68)	40.34 (9.58)
	Release	MI-PP	92.4 (13.4)	96.1 (12.9)	96.00 (12.30)	98.02 (13.00)
		PP-MI	96.9 (11.9)	95.2 (11.2)	96.45 (10.24)	95.50 (10.57)
		PP-only	96.52 (10.23)	97.56 (11.05)	96.77 (9.56)	95.78 (9.69)
Release time (sec)		MI-PP	0.176 (0.028)	0.170 (0.03)	0.17 (0.03)	0.18 (0.03)
		PP-MI	0.205 (0.03)	0.158 (0.03)	0.16 (0.02)	0.16 (0.02)
		PP-only	0.18 (0.04)	0.17 (0.04)	0.17 (0.04)	0.16 (0.04)

Angular velocity† (°/ sec)	MI-PP	329.8 (86.8)	365.6 (70.5)	370.75 (76.01)	364.20 (70.26)
	PP-MI	289.1 (69.8)	350.9 (73.2)	356.71 (81.60)	357.73 (76.19)
	PP-only	328.87 (61.87)	346.74 (115.05)	334.19 (85.32)	345.98 (88.35)

Appendix C: Skill transfer following MI-based practice

For the golf task, putting was performed using a standard putter and golf ball. Participants were instructed to putt the golf ball at a target (the flag hole, represented as a white circle, with alternating green and white target rings) 2.44m away from the starting point on an artificial indoor putting green (400 X 700 cm). Each testing block was comprised of 18 total trials, performed in three blocks of six trials. The order that the tasks were administered during each testing session was randomized and counterbalanced across participants. The primary outcome measure was points, using a ring-based system. Specifically, similar to (Smith et al., 2008), we considered the target to be 10 points, with each subsequent ring two less points. One point was awarded if the ball passed the halfway line on the putting green but did not land on any of the target rings. No points were awarded if the ball rolled off the putting green. To facilitate comparison between the three groups (MI-PP; PP-MI; and PP-only) and across the four time points (day 1, 5, 6, 10), total points across blocks were calculated for each participant.

As all data met the assumptions of ANOVA, we performed a 3 (group) X 4 (time point) ANOVA and characterised the extent to which learning occurred within each group via effect sizes (see Appendix X). A significant main effect was observed for time point (F(3,136) = 5.51, *p* = 0.001), although we did not observe a main effect of group (F(3,136) = 0.49, *p* = 0.69), nor interaction (F(6,136) = 0.64, *p* = 0.70).

Table 6.3

Means (and SDs) for each group on the golf putting (untrained transfer) task at each time point.

	Mean points (*SD*)			
Group	Day 1	Day 5	Day 6	Day 10
MI-PP	31.8 (*12.4*)	34.4 (*16.2*)	38.0 (*13.5*)	46.6 (*16.4*)
PP-MI	28.5 (*10.7*)	41.3 (*13.6*)	40.0 (*16.4*)	48.2 (*20.9*)
PP-PP	32.7 (*11.7*)	34.8 (*11.2*)	39.9 (*14.6*)	39.5 (*9.1*)

Table 6.4

Effect sizes conducted on data from Chapter 3 to characterise changes in performance for the golf putting (untrained transfer) task for the first half of training (day 5 minus day 1), retention (day 6 minus day 1), and overall (day 10 minus day 1). A positive effect size reflects an increase in points across training sessions.

	Cohen's *d*		
Group	Acquisition (day 5 minus 1)	Retention (day 6 minus 1)	Overall (day 10 minus 1)
MI-PP	0.45	0.48	1.01
PP-MI	1.04	0.83	1.19
PP-PP	0.18	0.54	0.65

Appendix D: Kinaesthetic Motor Imagery Script

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

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

As we mentioned before there are two ways to do motor imagery. The first is by picturing yourself performing the movement and the second is by picturing someone else doing the movement. For this study we want you to imagine yourself doing the movement.

Right now we want you to watch the video of the motor task so you can start to form a picture of yourself performing this task in your head.

Appendix E: Imagery Ability

The mean MIQ-RS score across a total of 132 participants was shown to be 76.4 (± 12.5), with a range of individual MIQ-RS scores (/98) reported in Chapters 2-4, as well as in prior work is min = 29, max = 98. Taking a score of ≥ 56 indicative of good imagery quality (i.e., representing an average rating of 4/7 per each item on the questionnaire), nine participants across all studies were noted to fall below this threshold, with only two participants noted to report ‘poor’ imagery quality (i.e., scoring < 42, or representative of a rating of 3/7 per each item).

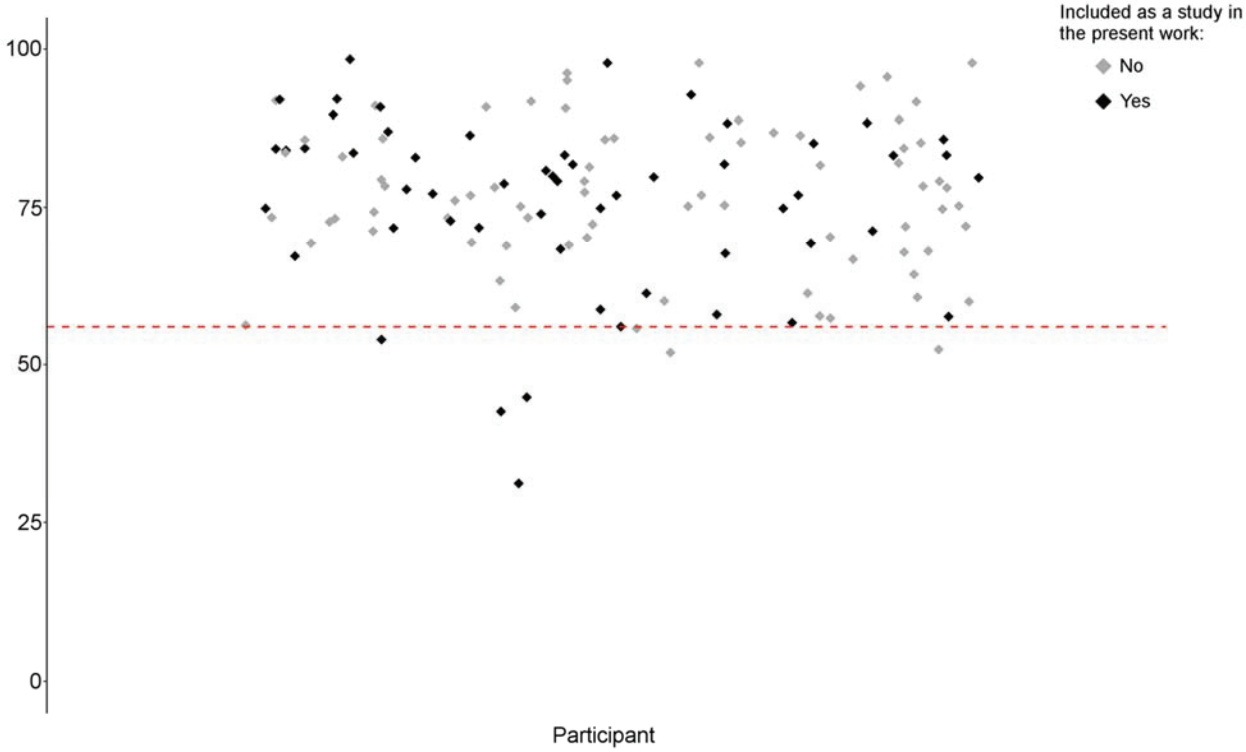


Figure 6.3 MIQ scores across all participants. Data reported is from Chapters 2-4 in conjunction with data taken from Kraeutner et al., 2018; 2019), and unpublished data from a study employing multiple assessments of imagery across the same participants. The red dashed line indicates a score of 56, indicating an average rating of 4/7 on each questionnaire item.

Appendix F: Imagery Use Questionnaire scores correlated with brain activation during motor imagery of a familiar task

Table 6.5

Results of Imagery Use Questionnaire scores against brain activation during 'teeth brushing'.

Hemisphere	Region	Voxels
R	Frontal Pole	6
R	Precentral Gyrus	15
R	Postcentral Gyrus	19
R	Lateral Occipital Cortex (inferior)	8
R	Intracalcarine Cortex	19
R	Precuneus Cortex'	6
R	Lingual Gyrus	48
R	Occipital Fusiform Gyrus	25
R	Occipital Pole	43

Note: Fewer than 5 significant voxels was not considered a significant cluster.

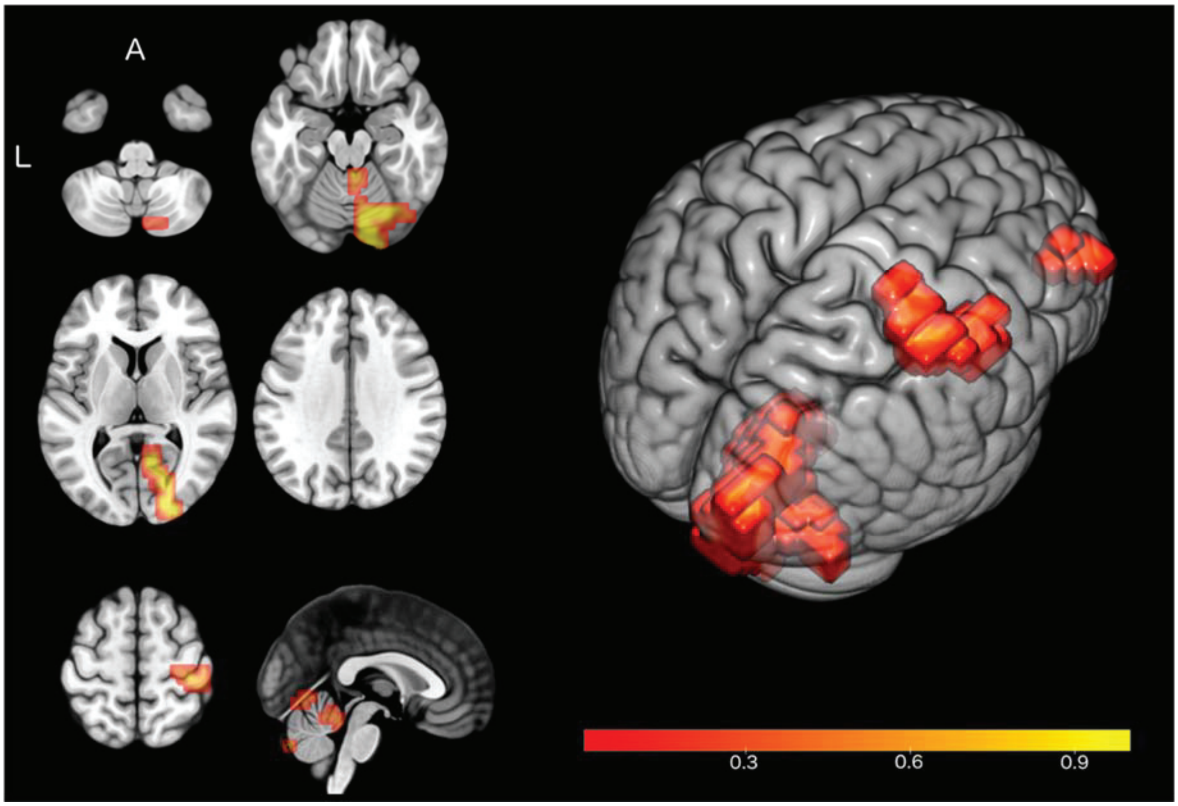
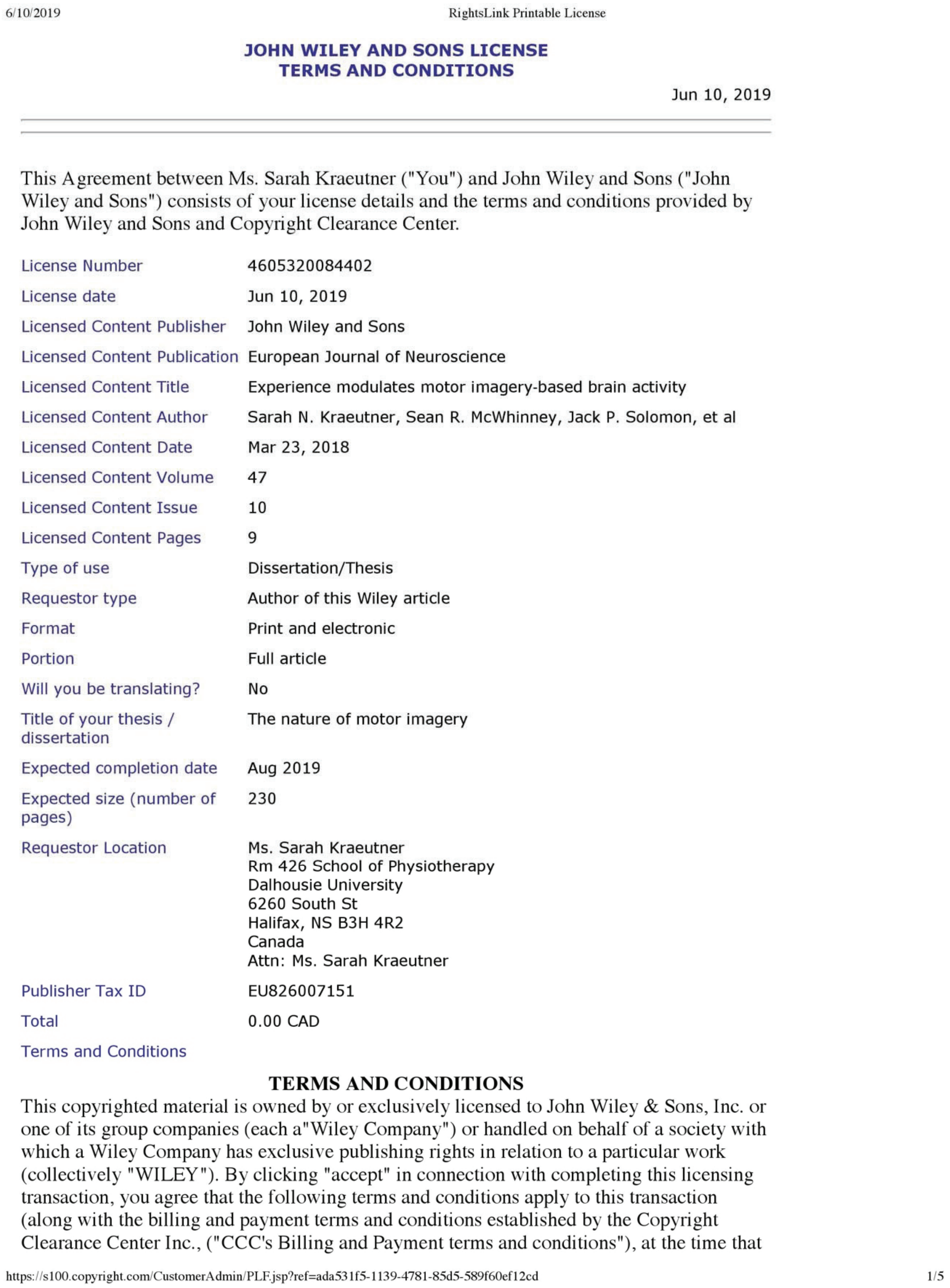


Figure 6.4 Regions where Imagery Use Questionnaire score is positively correlated with beamformer pseudo-z score, for MI of the teeth-brushing task. Only clusters with ≥5 voxels were considered significant and plotted.

Appendix G: Copyright release - Wiley



6/10/2019 RightsLink Printable License

JOHN WILEY AND SONS LICENSE
TERMS AND CONDITIONS

Jun 10, 2019

This Agreement between Ms. Sarah Kraeutner ("You") and John Wiley and Sons ("John Wiley and Sons") consists of your license details and the terms and conditions provided by John Wiley and Sons and Copyright Clearance Center.

License Number	4605320084402
License date	Jun 10, 2019
Licensed Content Publisher	John Wiley and Sons
Licensed Content Publication	European Journal of Neuroscience
Licensed Content Title	Experience modulates motor imagery-based brain activity
Licensed Content Author	Sarah N. Kraeutner, Sean R. McWhinney, Jack P. Solomon, et al
Licensed Content Date	Mar 23, 2018
Licensed Content Volume	47
Licensed Content Issue	10
Licensed Content Pages	9
Type of use	Dissertation/Thesis
Requestor type	Author of this Wiley article
Format	Print and electronic
Portion	Full article
Will you be translating?	No
Title of your thesis / dissertation	The nature of motor imagery
Expected completion date	Aug 2019
Expected size (number of pages)	230
Requestor Location	Ms. Sarah Kraeutner Rm 426 School of Physiotherapy Dalhousie University 6260 South St Halifax, NS B3H 4R2 Canada Attn: Ms. Sarah Kraeutner
Publisher Tax ID	EU826007151
Total	0.00 CAD
Terms and Conditions	

TERMS AND CONDITIONS

This copyrighted material is owned by or exclusively licensed to John Wiley & Sons, Inc. or one of its group companies (each a"Wiley Company") or handled on behalf of a society with which a Wiley Company has exclusive publishing rights in relation to a particular work (collectively "WILEY"). By clicking "accept" in connection with completing this licensing transaction, you agree that the following terms and conditions apply to this transaction (along with the billing and payment terms and conditions established by the Copyright Clearance Center Inc., ("CCC's Billing and Payment terms and conditions"), at the time that

https://s100.copyright.com/CustomerAdmin/PLF.jsp?ref=ada531f5-1139-4781-85d5-589f60ef12cd 1/5 you opened your RightsLink account (these are available at any time at http://myaccount.copyright.com).

Terms and Conditions

- The materials you have requested permission to reproduce or reuse (the "Wiley Materials") are protected by copyright.

- You are hereby granted a personal, non-exclusive, non-sub licensable (on a stand-alone basis), non-transferable, worldwide, limited license to reproduce the Wiley Materials for the purpose specified in the licensing process. This license, **and any CONTENT (PDF or image file) purchased as part of your order,** is for a one-time use only and limited to any maximum distribution number specified in the license. The first instance of republication or reuse granted by this license must be completed within two years of the date of the grant of this license (although copies prepared before the end date may be distributed thereafter). The Wiley Materials shall not be used in any other manner or for any other purpose, beyond what is granted in the license. Permission is granted subject to an appropriate acknowledgement given to the author, title of the material/book/journal and the publisher. You shall also duplicate the copyright notice that appears in the Wiley publication in your use of the Wiley Material. Permission is also granted on the understanding that nowhere in the text is a previously published source acknowledged for all or part of this Wiley Material. Any third party content is expressly excluded from this permission.

- With respect to the Wiley Materials, all rights are reserved. Except as expressly granted by the terms of the license, no part of the Wiley Materials may be copied, modified, adapted (except for minor reformatting required by the new Publication), translated, reproduced, transferred or distributed, in any form or by any means, and no derivative works may be made based on the Wiley Materials without the prior permission of the respective copyright owner.**For STM Signatory Publishers clearing permission under the terms of the STM Permissions Guidelines only, the terms of the license are extended to include subsequent editions and for editions in other languages, provided such editions are for the work as a whole in situ and does not involve the separate exploitation of the permitted figures or extracts,** You may not alter, remove or suppress in any manner any copyright, trademark or other notices displayed by the Wiley Materials. You may not license, rent, sell, loan, lease, pledge, offer as security, transfer or assign the Wiley Materials on a stand-alone basis, or any of the rights granted to you hereunder to any other person.

- The Wiley Materials and all of the intellectual property rights therein shall at all times remain the exclusive property of John Wiley & Sons Inc, the Wiley Companies, or their respective licensors, and your interest therein is only that of having possession of and the right to reproduce the Wiley Materials pursuant to Section 2 herein during the continuance of this Agreement. You agree that you own no right, title or interest in or to the Wiley Materials or any of the intellectual property rights therein. You shall have no rights hereunder other than the license as provided for above in Section 2. No right, license or interest to any trademark, trade name, service mark or other branding ("Marks") of WILEY or its licensors is granted hereunder, and you agree that you shall not assert any such right, license or interest with respect thereto

- NEITHER WILEY NOR ITS LICENSORS MAKES ANY WARRANTY OR REPRESENTATION OF ANY KIND TO YOU OR ANY THIRD PARTY, EXPRESS, IMPLIED OR STATUTORY, WITH RESPECT TO THE MATERIALS OR THE ACCURACY OF ANY INFORMATION CONTAINED IN THE

MATERIALS, INCLUDING, WITHOUT LIMITATION, ANY IMPLIED WARRANTY OF MERCHANTABILITY, ACCURACY, SATISFACTORY QUALITY, FITNESS FOR A PARTICULAR PURPOSE, USABILITY, INTEGRATION OR NON-INFRINGEMENT AND ALL SUCH WARRANTIES ARE HEREBY EXCLUDED BY WILEY AND ITS LICENSORS AND WAIVED BY YOU.

- WILEY shall have the right to terminate this Agreement immediately upon breach of this Agreement by you.
- You shall indemnify, defend and hold harmless WILEY, its Licensors and their respective directors, officers, agents and employees, from and against any actual or threatened claims, demands, causes of action or proceedings arising from any breach of this Agreement by you.
- IN NO EVENT SHALL WILEY OR ITS LICENSORS BE LIABLE TO YOU OR ANY OTHER PARTY OR ANY OTHER PERSON OR ENTITY FOR ANY SPECIAL, CONSEQUENTIAL, INCIDENTAL, INDIRECT, EXEMPLARY OR PUNITIVE DAMAGES, HOWEVER CAUSED, ARISING OUT OF OR IN CONNECTION WITH THE DOWNLOADING, PROVISIONING, VIEWING OR USE OF THE MATERIALS REGARDLESS OF THE FORM OF ACTION, WHETHER FOR BREACH OF CONTRACT, BREACH OF WARRANTY, TORT, NEGLIGENCE, INFRINGEMENT OR OTHERWISE (INCLUDING, WITHOUT LIMITATION, DAMAGES BASED ON LOSS OF PROFITS, DATA, FILES, USE, BUSINESS OPPORTUNITY OR CLAIMS OF THIRD PARTIES), AND WHETHER OR NOT THE PARTY HAS BEEN ADVISED OF THE POSSIBILITY OF SUCH DAMAGES. THIS LIMITATION SHALL APPLY NOTWITHSTANDING ANY FAILURE OF ESSENTIAL PURPOSE OF ANY LIMITED REMEDY PROVIDED HEREIN.
- Should any provision of this Agreement be held by a court of competent jurisdiction to be illegal, invalid, or unenforceable, that provision shall be deemed amended to achieve as nearly as possible the same economic effect as the original provision, and the legality, validity and enforceability of the remaining provisions of this Agreement shall not be affected or impaired thereby.
- The failure of either party to enforce any term or condition of this Agreement shall not constitute a waiver of either party's right to enforce each and every term and condition of this Agreement. No breach under this agreement shall be deemed waived or excused by either party unless such waiver or consent is in writing signed by the party granting such waiver or consent. The waiver by or consent of a party to a breach of any provision of this Agreement shall not operate or be construed as a waiver of or consent to any other or subsequent breach by such other party.
- This Agreement may not be assigned (including by operation of law or otherwise) by you without WILEY's prior written consent.
- Any fee required for this permission shall be non-refundable after thirty (30) days from receipt by the CCC.
- These terms and conditions together with CCC's Billing and Payment terms and conditions (which are incorporated herein) form the entire agreement between you and WILEY concerning this licensing transaction and (in the absence of fraud) supersedes all prior agreements and representations of the parties, oral or written. This Agreement

may not be amended except in writing signed by both parties. This Agreement shall be binding upon and inure to the benefit of the parties' successors, legal representatives, and authorized assigns.

- In the event of any conflict between your obligations established by these terms and conditions and those established by CCC's Billing and Payment terms and conditions, these terms and conditions shall prevail.

- WILEY expressly reserves all rights not specifically granted in the combination of (i) the license details provided by you and accepted in the course of this licensing transaction, (ii) these terms and conditions and (iii) CCC's Billing and Payment terms and conditions.

- This Agreement will be void if the Type of Use, Format, Circulation, or Requestor Type was misrepresented during the licensing process.

- This Agreement shall be governed by and construed in accordance with the laws of the State of New York, USA, without regards to such state's conflict of law rules. Any legal action, suit or proceeding arising out of or relating to these Terms and Conditions or the breach thereof shall be instituted in a court of competent jurisdiction in New York County in the State of New York in the United States of America and each party hereby consents and submits to the personal jurisdiction of such court, waives any objection to venue in such court and consents to service of process by registered or certified mail, return receipt requested, at the last known address of such party.

WILEY OPEN ACCESS TERMS AND CONDITIONS

Wiley Publishes Open Access Articles in fully Open Access Journals and in Subscription journals offering Online Open. Although most of the fully Open Access journals publish open access articles under the terms of the Creative Commons Attribution (CC BY) License only, the subscription journals and a few of the Open Access Journals offer a choice of Creative Commons Licenses. The license type is clearly identified on the article.

The Creative Commons Attribution License

The Creative Commons Attribution License (CC-BY) allows users to copy, distribute and transmit an article, adapt the article and make commercial use of the article. The CC-BY license permits commercial and non-

Creative Commons Attribution Non-Commercial License

The Creative Commons Attribution Non-Commercial (CC-BY-NC)License permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.(see below)

Creative Commons Attribution-Non-Commercial-NoDerivs License

The Creative Commons Attribution Non-Commercial-NoDerivs License (CC-BY-NC-ND) permits use, distribution and reproduction in any medium, provided the original work is properly cited, is not used for commercial purposes and no modifications or adaptations are made. (see below)

Use by commercial "for-profit" organizations

Use of Wiley Open Access articles for commercial, promotional, or marketing purposes requires further explicit permission from Wiley and will be subject to a fee.
Further details can be found on Wiley Online Library
http://olabout.wiley.com/WileyCDA/Section/id-410895.html

Other Terms and Conditions:

v1.10 Last updated September 2015

Questions? customercare@copyright.com or +1-855-239-3415 (toll free in the US) or +1-978-646-2777.

BIBLIOGRAPHY

Akaike H (1974) A new look at the statistical model identification. Ieee T Automat Contr 19:716–723.

Allan MS, Clause D, Pierre F, John K, Nathalie P (2015) Comparing Cerebellar and Motor Cortical Activity in Reaching and Grasping. Can J Neurological Sci J Can Des Sci Neurologiques 20:S53–S61.

Amemiya K, Ishizu T, Ayabe T, Kojima S (2010) Effects of motor imagery on intermanual transfer: A near-infrared spectroscopy and behavioural study. Brain Research 1343:93–103.

Andersson JLR, Skare S, Ashburner J (2003) How to correct susceptibility distortions in spin-echo echo-planar images: application to diffusion tensor imaging. NeuroImage 20:870–888.

Annett J (1995) Motor imagery: Perception or action? Neuropsychologia 33:1395–1417.

Apolinário-Souza T, Romano-Silva MA, de Miranda DM, Malloy-Diniz LF, Benda RN, Ugrinowitsch H, Lage GM (2016) The primary motor cortex is associated with learning the absolute, but not relative, timing dimension of a task: A tDCS study. Physiology & Behavior 160:18–25.

Ashe J, Georgopoulos AP (1994) Movement Parameters and Neural Activity in Motor Cortex and Area 5. Cereb Cortex 4:590–600.

Baeck J-S, Kim Y-T, Seo J-H, Ryeom H-K, Lee J, Choi S-M, Woo M, Kim W, Kim JG, Chang Y (2012) Brain activation patterns of motor imagery reflect plastic changes associated with intensive shooting training. Behavioural Brain Research 234:26–32.

Bapi RS, Doya K, Harner AM (2000) Evidence for effector independent and dependent representations and their differential time course of acquisition during motor sequence learning. Exp Brain Res 132:149–162.

Bapi RS, Miyapuram KP, Graydon FX, Doya K (2006) fMRI investigation of cortical and subcortical networks in the learning of abstract and effector-specific representations of motor sequences. NeuroImage 32:714–727.

Bar RJ, DeSouza JFX (2016) Tracking Plasticity: Effects of Long-Term Rehearsal in Expert Dancers Encoding Music to Movement D'Ausilio A, ed. PLoS ONE 11:e0147731.

Barclay Goddard RE, Stevenson TJ, Poluha W, Thalman L (2011) Mental practice for treating upper extremity deficits in individuals with hemiparesis after stroke Cochrane Stroke Group, ed. Cochrane Database of Systematic Reviews 25:501.

Bastian AJ (2006) Learning to predict the future: the cerebellum adapts feedforward movement control. Curr Opin Neurobiol 16:645–649.

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. J Stat Soft 67.

Binkofski F, Buxbaum LJ (2013) Two action systems in the human brain. Brain and Language 127:222–229.

Blakemore S-J, Sirigu A (2003) Action prediction in the cerebellum and in the parietal lobe. Exp Brain Res 153:239–245.

Blakemore S-J, Wolpert DM, Frith CD (1998) Central cancellation of self-produced tickle sensation. Nat Neurosci 1:635–640.

Boe S, Kraeutner S (2017) Assessing Motor Imagery Ability Through Imagery-Based Learning: An Overview and Introduction to Miscreen, a Mobile App for Imagery Assessment. Imagination Cognition Personality:027623661773504.

Boe S, Gionfriddo A, Kraeutner S, Tremblay A, Little G, Bardouille T (2014) Laterality of brain activity during motor imagery is modulated by the provision of source level neurofeedback. NeuroImage 101:159–167.

Boe SG, Cassidy RJ, McIlroy WE, Graham SJ (2012) Single session motor learning demonstrated using a visuomotor task: Evidence from fMRI and behavioural analysis. Journal of Neuroscience Methods 209:308–319.

Bovend'Eerdt TJH, Dawes H, Sackley C, Wade DT (2012) Practical research-based guidance for motor imagery practice in neurorehabilitation. Disability and Rehabilitation 34:2192–2200.

Braun S, Kleynen M, Schols J, Schack T, Beurskens A, Wade D (2008) Using mental practice in stroke rehabilitation: a framework. Clin Rehabil 22:579–591.

Braun S, Kleynen M, van Heel T, Kruithof N, Wade D, Beurskens A (2013) The effects of mental practice in neurological rehabilitation; a systematic review and meta-analysis. Front Hum Neurosci 7:390.

Brookes MJ, Hale JR, Zumer JM, Stevenson CM, Francis ST, Barnes GR, Owen JP, Morris PG, Nagarajan SS (2011) Measuring functional connectivity using MEG: Methodology and comparison with fcMRI. NeuroImage 56:1082–1104.

Brooks JX, Cullen KE (2013) The Primate Cerebellum Selectively Encodes Unexpected Self-Motion. Current Biology 23:947–955.

Brown RM, Palmer C (2013) Auditory and motor imagery modulate learning in music performance. Front Hum Neurosci 7:320.

Burianová H, Marstaller L, Sowman P, Tesan G, Rich AN, Williams M, Savage G, Johnson BW (2013) Multimodal functional imaging of motor imagery using a novel paradigm. NeuroImage 71:50–58.

Butler AJ, Cazeaux J, Fidler A, Jansen J, Lefkove N, Gregg M, Hall C, Easley KA, Shenvi N, Wolf SL (2012) The Movement Imagery Questionnaire-Revised, Second Edition (MIQ-RS) Is a Reliable and Valid Tool for Evaluating Motor Imagery in Stroke Populations. Evidence-Based Complementary and Alternative Medicine 2012:1–11.

Buxbaum LJ, Johnson-Frey SH, Bartlett-Williams M (2005a) Deficient internal models for planning hand–object interactions in apraxia. Neuropsychologia 43:917–929.

Buxbaum LJ, Kyle K, Grossman M, Coslett B (2007) Left Inferior Parietal Representations for Skilled Hand-Object Interactions: Evidence from Stroke and Corticobasal Degeneration. Cortex 43:411–423.

Buxbaum LJ, Kyle KM, Menon R (2005b) On beyond mirror neurons: Internal representations subserving imitation and recognition of skilled object-related actions in humans. Cognitive Brain Research 25:226–239.

Buxbaum LJ, Kyle KM, Tang K, Detre JA (2006) Neural substrates of knowledge of hand postures for object grasping and functional object use: Evidence from fMRI. Brain Research 1117:175–185.

Carrasco G, Cantalapiedra A (2016) Effectiveness of motor imagery or mental practice in functional recovery after stroke: a systematic review. Neurología (English Edition) 31(1):43-52.

Censor N, Dayan E, Cohen LG (2014) Cortico-subcortical neuronal circuitry associated with reconsolidation of human procedural memories. Cortex 58:281–288.

Chang Y, Lee JJ, Seo J-H, Song HJ, Kim Y-T, Lee HJ, Kim HJ, Lee J, Kim W, Woo M, Kim JG (2010) Neural correlates of motor imagery for elite archers. Nmr Biomed 21:n/a–n/a.

Collet C, Guillot A, Lebon F, MacIntyre T, Moran A (2011) Measuring Motor Imagery Using Psychometric, Behavioral, and Psychophysiological Tools. Exercise Sport Sci R 39:85–92.

Collins D, Carson HJ (2017) The future for PETTLEP: a modern perspective on an effective and established tool. Current Opinion in Psychology 16:12–16.

Cowper-Smith C, Lau E, Helmick C, Eskes G, Westwood D (2010) Neural Coding of Movement Direction in the Healthy Human Brain. Plos One 5:e13330.

Culham JC, Cavina-Pratesi C, Singhal A (2006) The role of parietal cortex in visuomotor control: What have we learned from neuroimaging? Neuropsychologia 44:2668–2684.

Cumming J, Eaves DL (2018) The Nature, Measurement, and Development of Imagery Ability. Imagination, Cognition and Personality 37:375–393.

Cunnington R, Windischberger C, Deecke L, Moser E (2003) The preparation and readiness for voluntary movement: a high-field event-related fMRI study of the Bereitschafts-BOLD response. NeuroImage 20:404–412.

Cunnington R, Windischberger C, Moser E (2005) Premovement activity of the pre-supplementary motor area and the readiness for action: Studies of time-resolved event-related functional MRI. Human Movement Science 24:644–656.

Dahm SF, Rieger M (2019) Is imagery better than reality? Performance in imagined dart throwing. Human Movement Science 66:38–52.

Dayan E, Cohen LG (2011) Neuroplasticity Subserving Motor Skill Learning. Neuron 72:443–454.

de Lange FP, Roelofs K, Toni I (2008) Motor imagery: A window into the mechanisms and alterations of the motor system. Cortex 44:494–506.

de Vries S, Tepper M, Feenstra W, Oosterveld H, Boonstra AM, Otten B (2013) Motor imagery ability in stroke patients: the relationship between implicit and explicit motor imagery measures. Front Hum Neurosci 7:790.

Debarnot U, Sperduti M, Di Rienzo F, Guillot A (2014) Experts bodies, experts minds: How physical and mental training shape the brain. Front Hum Neurosci 8:73.

Decety J (1996) Do imagined and executed actions share the same neural substrate? Cognitive Brain Research 3:87–93.

Deecke L, Kornhuber HH (1978) An electrical sign of participation of the mesial “supplementary” motor cortex in human voluntary finger movement. Brain Research 159:473–476.

Del Percio C, Rossini PM, Marzano N, Iacoboni M, Infarinato F, Aschieri P, Lino A, Fiore A, Toran G, Babiloni C, Eusebi F (2008) Is there a “neural efficiency” in athletes? A high-resolution EEG study. NeuroImage 42:1544–1553.

Desikan RS, Ségonne F, Fischl B, Quinn BT, Dickerson BC, Blacker D, Buckner RL, Dale AM, Maguire RP, Hyman BT, Albert MS, Killiany RJ (2006) An automated labeling system for subdividing the human cerebral cortex on MRI scans into gyral based regions of interest. NeuroImage 31:968–980.

Di Rienzo F, Debarnot U, Daligault S, Saruco E, Delpuech C, Doyon J, Collet C, Guillot A (2016) Online and Offline Performance Gains Following Motor Imagery Practice: A Comprehensive Review of Behavioral and Neuroimaging Studies. Front Hum Neurosci 10:30.

Didier JJ, Li L, Magill RA (2013) Environmental Context Affects Outcome and Kinematic Changes at Different Rates during Skill Learning. Percept Mot Skills 116:953–968.

Diwakar M, Huang M-X, Srinivasan R, Harrington DL, Robb A, Angeles A, Muzzatti L, Pakdaman R, Song T, Theilmann RJ, Lee RR (2011a) Dual-Core Beamformer for obtaining highly correlated neuronal networks in MEG. NeuroImage 54:253–263.

Diwakar M, Tal O, Liu TT, Harrington DL, Srinivasan R, Muzzatti L, Song T, Theilmann RJ, Lee RR, Huang M-X (2011b) Accurate reconstruction of temporal correlation for neuronal sources using the enhanced dual-core MEG beamformer. NeuroImage 56:1918–1928.

Doyon J, Benali H (2005) Reorganization and plasticity in the adult brain during learning of motor skills. Curr Opin Neurobiol 15:161–167.

Doyon J, Orban P, Barakat M, Debas K, Lungu O, Albouy G, Fogel S, Proulx S, Laventure S, Deslauriers J, Duchesne C, Carrier J, Benali H (2011) Functional brain plasticity associated with motor learning. Med Sci (Paris) 27:413–420.

Doyon J, Song AW, Karni A, Lalonde F, Adams MM, Ungerleider LG (2002) Experience-dependent changes in cerebellar contributions to motor sequence learning. Proc Natl Acad Sci USA 99:1017–1022.

Driskell JE, Copper C, Moran A (1994) Does mental practice enhance performance? J Appl Psychol 79:481–492.

Duann J-R, Chiou J-C (2016) A Comparison of Independent Event-Related Desynchronization Responses in Motor-Related Brain Areas to Movement Execution, Movement Imagery, and Movement Observation Yao D, ed. PLoS ONE 11:e0162546.

Eaves DL, Emerson JR, Binks JA, Scott MW, Kenny RPW (2018) Imagery ability: the individual difference gradient and novel training methods (Commentary on Kraeutner et al. (2018)). Eur J Neurosci 47:1219–1220.

Edwards B, Waterhouse J, Atkinson G, Reilly T (2007a) Effects of time of day and distance upon accuracy and consistency of throwing darts. J Sport Sci 25:1531–1538.

Edwards BJ, Lindsay K, Waterhouse J (2007b) Effect of time of day on the accuracy and consistency of the badminton serve. Ergonomics 48:1488–1498.

Elliott R (2000) Dissociable Functions in the Medial and Lateral Orbitofrontal Cortex: Evidence from Human Neuroimaging Studies. Cerebral Cortex 10:308–317.

Espinoza E, Smith AM (1990) Purkinje cell simple spike activity during grasping and lifting objects of different textures and weights. J Neurophysiol 64:698–714.

Evans C, Edwards MG, Taylor LJ, Ietswaart M (2016) Perceptual decisions regarding object manipulation are selectively impaired in apraxia or when tDCS is applied over the left IPL. Neuropsychologia 86:153–166.

Fitts, P. M., Posner, M. I. (1967). Human performance. Belmont, CA: Brooks/Cole.

Flash T, Bizzi E (2016) Cortical circuits and modules in movement generation: experiments and theories. Curr Opin Neurobiol 41:174–178.

Floyer-Lea A, Matthews PM (2005) Distinguishable Brain Activation Networks for Short- and Long-Term Motor Skill Learning. J Neurophysiol 94:512–518.

Formaggio E, Storti SF, Cerini R, Fiaschi A, Manganotti P (2010) Brain oscillatory activity during motor imagery in EEG-fMRI coregistration. Magnetic Resonance Imaging 28:1403–1412.

Frank C, Land WM, Popp C, Schack T (2014) Mental Representation and Mental Practice: Experimental Investigation on the Functional Links between Motor Memory and Motor Imagery Urgesi C, ed. PLoS ONE 9:e95175.

Frank C, Land WM, Schack T (2013) Mental representation and learning: The influence of practice on the development of mental representation structure in complex action. Psychology of Sport and Exercise 14:353–361.

Frank C, Land WM, Schack T (2016) Perceptual-Cognitive Changes During Motor Learning: The Influence of Mental and Physical Practice on Mental Representation, Gaze Behavior, and Performance of a Complex Action. Front Psychol 6:350.

Frank C, Schack T (2017) The Representation of Motor (Inter)action, States of Action, and Learning: Three Perspectives on Motor Learning by Way of Imagery and Execution. Front Psychol 8:9.

Frazier JA, Chiu S, Breeze JL, Makris N, Lange N, Kennedy DN, Herbert MR, Bent EK, Koneru VK, Dieterich ME, Hodge SM, Rauch SL, Grant PE, Cohen BM, Seidman LJ, Caviness VS, Biederman J (2005) Structural Brain Magnetic Resonance Imaging of Limbic and Thalamic Volumes in Pediatric Bipolar Disorder. AJP 162:1256–1265.

Gallivan JP, McLean DA, Smith FW, Culham JC (2011) Decoding Effector-Dependent and Effector-Independent Movement Intentions from Human Parieto-Frontal Brain Activity. J Neurosci 31:17149–17168.

Gao JH, Parsons LM, Bower JM, Xiong J, Li J, Fox PT (1996) Cerebellum Implicated in Sensory Acquisition and Discrimination Rather Than Motor Control. Science 272:545–547.

Gauthier I, Skudlarski P, Gore JC, Anderson AW (2000) Expertise for cars and birds recruits brain areas involved in face recognition. Nat Neurosci 3:191–197.

Gentili R, Han CE, Schweighofer N, Papaxanthis C (2010) Motor Learning Without Doing: Trial-by-Trial Improvement in Motor Performance During Mental Training. J Neurophysiol 104:774–783.

Gentili R, Papaxanthis C, Pozzo T (2006) Improvement and generalization of arm motor performance through motor imagery practice. Neuroscience 137:761–772.

Georgopoulos A, Schwartz A, Kettner R (1986) Neuronal population coding of movement direction. Science 233:1416–1419.

Georgopoulos AP (1990) Neural Coding of the Direction of Reaching and a Comparison with Saccadic Eye Movements. Cold Spring Harb Sym 55:849–859.

Gibson RM, Chennu S, Owen AM, Cruse D (2014) Complexity and familiarity enhance single-trial detectability of imagined movements with electroencephalography. Clinical Neurophysiology 125:1556–1567.

Goldstein JM, Seidman LJ, Makris N, Ahern T, O'Brien LM, Caviness VS Jr., Kennedy DN, Faraone SV, Tsuang MT (2007) Hypothalamic Abnormalities in Schizophrenia: Sex Effects and Genetic Vulnerability. Biological Psychiatry 61:935–945.

Goodale MA, Milner AD (1992) Separate visual pathways for perception and action. Trends in Neurosciences 15:20–25.

Goodale MA, Westwood DA (2004) An evolving view of duplex vision: separate but interacting cortical pathways for perception and action. Curr Opin Neurobiol 14:203–211.

Grafton ST, Hazeltine E, Ivry RB (1998) Abstract and Effector-Specific Representations of Motor Sequences Identified with PET. J Neurosci 18:9420–9428.

Grafton ST, Hazeltine E, Ivry RB (2002) Motor sequence learning with the nondominant left hand. Exp Brain Res 146:369–378.

Grafton ST, Mazziotta JC, Presty S, Friston KJ, Frackowiak RS, Phelps ME (1992) Functional anatomy of human procedural learning determined with regional cerebral blood flow and PET. J Neurosci 12:2542–2548.

Gregg M, Hall C, Butler A (2010) The MIQ-RS: A Suitable Option for Examining Movement Imagery Ability. Evidence-Based Complementary and Alternative Medicine 7:249–257.

Gregg M, Hall C, Nederhof E (2005) The Imagery Ability, Imagery Use, and Performance Relationship. Sport Psychologist 19:93–99.

Greiner J, Schoenfeld MA, Liepert J (2014) Assessment of mental chronometry (MC) in healthy subjects. Archives of Gerontology and Geriatrics 58:226–230.

Grèzes J, Decety J (2000) Functional anatomy of execution, mental simulation, observation, and verb generation of actions: A meta-analysis. Hum Brain Mapp 12:1–19.

Grosprêtre S, Lebon F, Papaxanthis C, Martin A (2016) New evidence of corticospinal network modulation induced by motor imagery. J Neurophysiol 115:1279–1288.

Grosprêtre S, Lebon F, Papaxanthis C, Martin A (2019) Spinal plasticity with motor imagery practice. J Physiology 597:921–934.

Guo Z, Li A, Yu L (2017) “Neural Efficiency” of Athletes’ Brain during Visuo-Spatial Task: An fMRI Study on Table Tennis Players. Front Behav Neurosci 11:1109.

Haggard P, Whitford B (2004) Supplementary motor area provides an efferent signal for sensory suppression. Cognitive Brain Research 19:52–58.

Hall C, Rodgers W, Barr K (1990) The use of imagery by athletes in selected sports. The Sport Psychologist 4:1–10.

Hanakawa T, Dimyan MA, Hallett M (2008) Motor Planning, Imagery, and Execution in the Distributed Motor Network: A Time-Course Study with Functional MRI. Cereb Cortex 18:2775–2788.

Hancock GR, Butler MS, Fischman MG (1995) On the Problem of Two-Dimensional Error Scores: Measures and Analyses of Accuracy, Bias, and Consistency. J Motor Behav 27:241–250.

Hansen C, Rezzoug N, Gorce P, Isableu B (2012) Is the time of release during a precision throwing task, predictable? Comput Method Biomec 15:250–252.

Hardwick RM, Caspers S, Eickhoff SB, Swinnen SP (2018) Neural correlates of action: Comparing meta-analyses of imagery, observation, and execution. Neuroscience and Biobehavioral Reviews 94:31–44.

Hardwick RM, Rottschy C, Miall RC, Eickhoff SB (2013) A quantitative meta-analysis and review of motor learning in the human brain. NeuroImage 67:283–297.

Haufler AJ, Spalding TW, Santa Maria DL, Hatfield BD (2000) Neuro-cognitive activity during a self-paced visuospatial task: comparative EEG profiles in marksmen and novice shooters. Biological Psychology 53:131–160.

Hayes SM, Ryan L, Schnyer DM, Nadel L (2004) An fMRI Study of Episodic Memory: Retrieval of Object, Spatial, and Temporal Information. Behav Neurosci 118:885–896.

Hétu S, Grégoire M, Saimpont A, Coll M-P, Eugène F, Michon P-E, Jackson PL (2013) The neural network of motor imagery: An ALE meta-analysis. Neuroscience and Biobehavioral Reviews 37:930–949.

Hikosaka O, Nakamura K, Sakai K, Nakahara H (2002) Central mechanisms of motor skill learning. Curr Opin Neurobiol 12:217–222.

Holmes P, Calmels C (2008) A Neuroscientific Review of Imagery and Observation Use in Sport. J Motor Behav 40:433–445.

Holmes PS, Collins DJ (2001) The PETTLEP Approach to Motor Imagery: A Functional Equivalence Model for Sport Psychologists. Journal of Applied Sport Psychology 13:60–83.

Hovington CL, Brouwer B (2010) Guided Motor Imagery in Healthy Adults and Stroke: Does Strategy Matter? Neurorehab Neural Re 24:851–857.

Ietswaart M, Johnston M, Dijkerman HC, Joice S, Scott CL, MacWalter RS, Hamilton SJC (2011) Mental practice with motor imagery in stroke recovery: randomized controlled trial of efficacy. Brain 134:1373–1386.

Ingram TGJ, Kraeutner SN, Solomon JP, Westwood DA, Boe SG (2016) Skill acquisition via motor imagery relies on both motor and perceptual learning. Behav Neurosci 130:252–260.

Ingram TGJ, Solomon JP, Westwood DA, Boe SG (2019) Movement related sensory feedback is not necessary for learning to execute a motor skill. Behavioural Brain Research 359:135–142.

Jackson PL, Lafleur MF, Malouin F, Richards CL, Doyon J (2003) Functional cerebral reorganization following motor sequence learning through mental practice with motor imagery. NeuroImage 20:1171–1180.

Jeannerod M (1995) Mental imagery in the motor context. Neuropsychologia 33:1419–1432.

Jeannerod M (2001) Neural Simulation of Action: A Unifying Mechanism for Motor Cognition. NeuroImage 14:S103–S109.

Jeannerod M (2010) The representing brain: Neural correlates of motor intention and imagery. Behavioral and Brain Sciences 17:187–202.

Jeannerod M, Decety J (1995) Mental motor imagery: a window into the representational stages of action. Curr Opin Neurobiol 5:727–732.

Jenkins IH, Brooks DJ, Nixon PD, Frackowiak RS, Passingham RE (1994) Motor sequence learning: a study with positron emission tomography. J Neurosci 14:3775–3790.

Jenkinson M, Bannister P, Brady M, Smith S (2002) Improved Optimization for the Robust and Accurate Linear Registration and Motion Correction of Brain Images. NeuroImage 17:825–841.

Johansson BB (2010) Current trends in stroke rehabilitation. A review with focus on brain plasticity. Acta neurologica Scandinavica 123:147–159.

Jones L, Stuth G (1997) The uses of mental imagery in athletics: An overview. Applied and Preventive Psychology 6:101–115.

Jueptner M, Ottinger S, Fellows SJ, Adamschewski J, Flerich L, Müller SP, Diener HC, Thilmann AF, Weiller C (1997) The Relevance of Sensory Input for the Cerebellar Control of Movements. NeuroImage 5:41–48.

Kandel, E. R., Schwartz, J. H., Jessell, T. M. (2000). Principles of neural science (4th ed.). NEW YORK: McGraw-Hill, Health Professions Division.

Karni A, Meyer G, Rey-Hipolito C, Jezzard P, Adams MM, Turner R, Ungerleider LG (1998) The acquisition of skilled motor performance: Fast and slow experience-driven changes in primary motor cortex. Proc Natl Acad Sci USA 95:861–868.

Kawamichi H, Kikuchi Y, Endo H, Takeda T, Yoshizawa S (1998) Temporal structure of implicit motor imagery in visual hand-shape discrimination as revealed by MEG. Neuroreport 9:1127–1132.

Kelly AMC, Garavan H (2004) Human Functional Neuroimaging of Brain Changes Associated with Practice. Cereb Cortex 15:1089–1102.

Kilteni K, Andersson BJ, Houborg C, Ehrsson HH (2018) Motor imagery involves predicting the sensory consequences of the imagined movement. Nat Commun 9:187.

Kim J, Lee HM, Kim WJ, Park HJ, Kim SW, Moon DH, Woo M, Tennant LK (2008) Neural correlates of pre-performance routines in expert and novice archers. Neuroscience Letters 445:236–241.

Kim T, Frank C, Schack T (2017) A Systematic Investigation of the Effect of Action Observation Training and Motor Imagery Training on the Development of Mental Representation Structure and Skill Performance. Front Hum Neurosci 11:173.

Kohl RM, Roenker DL (1980) Bilateral Transfer as a Function of Mental Imagery. J Motor Behav 12:197–206.

Kohl RM, Roenker DL (1983) Mechanism Involvement During Skill Imagery. J Motor Behav 15:179–190.

Kraeutner S, Gionfriddo A, Bardouille T, Boe S (2014) Motor imagery-based brain activity parallels that of motor execution: Evidence from magnetic source imaging of cortical oscillations. Brain Research 1588:81–91.

Kraeutner SN, El-Serafi M, Lee J, Boe SG (2019) Disruption of motor imagery performance following inhibition of the left inferior parietal lobe. Neuropsychologia 127:106–112.

Kraeutner SN, Gaughan TC, Eppler SN, Boe SG (2017a) Motor imagery-based implicit sequence learning depends on the formation of stimulus-response associations. Acta Psychol (Amst) 178:48–55.

Kraeutner SN, Ingram TGJ, Boe SG (2017b) The effector independent nature of motor imagery: Evidence from rTMS induced inhibition to the primary motor cortices. Neuropsychologia 97:1–8.

Kraeutner SN, Keeler LT, Boe SG (2016b) Motor imagery-based skill acquisition disrupted following rTMS of the inferior parietal lobule. Exp Brain Res 234:397–407.

Kraeutner SN, MacKenzie LA, Westwood DA, Boe SG (2016a) Characterizing skill acquisition through motor imagery with no prior physical practice. J Exp Psychology Hum Percept Perform 42:257–265.

Kraeutner SN, McWhinney SR, Solomon JP, Dithurbide L, Boe SG (2018) Experience modulates motor imagery-based brain activity. Eur J Neurosci 47:1221–1229.

Kremer P, Spittle M, McNeil D, Shinners C (2009) Amount of Mental Practice and Performance of a Simple Motor Task. Percept Mot Skills 109:347–356.

Kumar A, Tanaka Y, Grigoriadis A, Grigoriadis J, Trulsson M, Svensson P (2017) Training-induced dynamics of accuracy and precision in human motor control. Sci Rep 7:644.

Lacourse MG, Orr ELR, Cramer SC, Cohen MJ (2005) Brain activation during execution and motor imagery of novel and skilled sequential hand movements. NeuroImage 27:505–519.

Lacourse MG, Turner JA, Randolph-Orr E, Schandler SL, Cohen MJ (2004) Cerebral and cerebellar sensorimotor plasticity following motor imagery-based mental practice of a sequential movement. J Rehabil Res Dev 41:505–524.

Lafleur MF, Jackson PL, Malouin F, Richards CL, Evans AC, Doyon J (2002) Motor Learning Produces Parallel Dynamic Functional Changes during the Execution and Imagination of Sequential Foot Movements. NeuroImage 16:142–157.

Land WM, Liu B, Cordova A, Fang M, Huang Y, Yao WX (2016) Effects of Physical Practice and Imagery Practice on Bilateral Transfer in Learning a Sequential Tapping Task Jaencke L, ed. PLoS ONE 11:e0152228.

Lebon F, Lotze M, Stinear CM, Byblow WD (2012) Task-Dependent Interaction between Parietal and Contralateral Primary Motor Cortex during Explicit versus Implicit Motor Imagery Wenderoth N, ed. PLoS ONE 7:e37850.

Lee TD (1988) Transfer-Appropriate Processing: A Framework for Conceptualizing Practice Effects in Motor Learning. Advances in Psychology 50:201–215.

Lehericy S, Benali H, Van de Moortele PF, Pelegrini-Issac M, Waechter T, Ugurbil K, Doyon J (2005) Distinct basal ganglia territories are engaged in early and advanced motor sequence learning. Proc Natl Acad Sci USA 102:12566–12571.

Li C-SR, Padoa-Schioppa C, Bizzi E (2001) Neuronal Correlates of Motor Performance and Motor Learning in the Primary Motor Cortex of Monkeys Adapting to an External Force Field. Neuron 30:593–607.

Li F, Zhang T, Li B-J, Zhang W, Zhao J, Song L-P (2018) Motor imagery training induces changes in brain neural networks in stroke patients. Neural Regen Res 13:1771–1781.

Lin C-HJ, Chiang MC, Knowlton BJ, Iacoboni M, Udompholkul P, Wu AD (2012) Interleaved practice enhances skill learning and the functional connectivity of fronto-parietal networks. Human Brain Mapping 34:1542–1558.

Liu KP, Chan CC, Lee TM, Hui-Chan CW (2004) Mental imagery for promoting relearning for people after stroke: A randomized controlled trial11No party having a direct interest in the results of the research supporting this article has or will confer a benefit on the author(s) or on any organization with which the author(s) is/are associated. Arch Phys Med Rehabil 85:1403–1408.

Lohse KR, Healy AF, Sherwood D (2010a) Mental Practice in the Intermanual Transfer of Motor Skills. Journal of Imagery Research in Sport and Physical Activity 5:6.

Lohse KR, Sherwood DE, Healy AF (2010b) How changing the focus of attention affects performance, kinematics, and electromyography in dart throwing. Human Movement Science 29:542–555.

Machado S, Lattari E, Paes F, Rocha NBF, Nardi AE, Arias-Carrión O, Mura G, Yuan T-F, Carta MG, Campos C (2016) Mental Practice Combined with Motor Rehabilitation to Treat Upper Limb Hemiparesis of Post-Stroke Patients: Clinical and Experimental Evidence. Clin Pract Epidemiology Ment Heal 12:9–13.

MacIntyre T, Madan C, Moran A, Collet C, Guillot A (2018) Motor imagery, performance and motor rehabilitation. Progress In Brain Research 240:141-159.

MacKay DG (1982) The problems of flexibility, fluency, and speed-accuracy trade-off in skilled behavior. Psychological Review 89:483–506.

Makris N, Goldstein JM, Kennedy D, Hodge SM, Caviness VS, Faraone SV, Tsuang MT, Seidman LJ (2006) Decreased volume of left and total anterior insular lobule in schizophrenia. Schizophrenia Research 83:155–171.

Malouin F, Jackson PL, Richards CL (2013) Towards the integration of mental practice in rehabilitation programs. A critical review. Front Hum Neurosci 7:576.

Matsuzaka Y, Picard N, Strick PL (2007) Skill Representation in the Primary Motor Cortex After Long-Term Practice. J Neurophysiol 97:1819–1832.

McAvinue LP, Robertson IH (2008) Measuring motor imagery ability: A review. European Journal of Cognitive Psychology 20:232–251.

McDonald PV, van Emmerik REA, Newell KM (1989) The Effects of Practice on Limb Kinematics in a Throwing Task. J Motor Behav 21:245–264.

McInnes K, Friesen C, Boe S (2016) Specific Brain Lesions Impair Explicit Motor Imagery Ability: A Systematic Review of the Evidence. Arch Phys Med Rehabil 97:478–489.e1.

Mendoza D, Wichman H (2016) “Inner” Darts: Effects of Mental Practice on Performance of Dart Throwing. Percept Mot Skills 47:1195–1199.

Miall RC, Wolpert DM (1996) Forward Models for Physiological Motor Control. Neural Networks 9:1265–1279.

Milton J, Small SL, Solodkin A (2008) Imaging motor imagery: Methodological issues related to expertise. Methods 45:336–341.

Milton J, Solodkin A, Hlustik P, Small SL (2007) The mind of expert motor performance is cool and focused. NeuroImage 35:804–813.

Mizuguchi N, Nakata H, Kanosue K (2014) Effector-independent brain activity during motor imagery of the upper and lower limbs: An fMRI study. Neuroscience Letters 581:69–74.

Moran A, Guillot A, MacIntyre T, Collet C (2011) Re-imagining motor imagery: Building bridges between cognitive neuroscience and sport psychology. British Journal of Psychology 103:224–247.

Müller F, Dichgans J (1994) Dyscoordination of pinch and lift forces during grasp in patients with cerebellar lesions. Exp Brain Res 101:485–492.

Munzert J, Zentgraf K (2009) Motor imagery and its implications for understanding the motor system. In: How are actions physically implemented?, pp 219–229 Progress in Brain Research. Elsevier.

Nachev P, Kennard C, Husain M (2008) Functional role of the supplementary and pre-supplementary motor areas. Nat Rev Neurosci 9:856–869.

Nakata H, Yoshie M, Miura A, Kudo K (2010) Characteristics of the athletes' brain: Evidence from neurophysiology and neuroimaging. Brain Research Reviews 62:197–211.

Nelson-Wong E, Howarth S, Winter DA, Callaghan JP (2009) Application of Autocorrelation and Cross-correlation Analyses in Human Movement and Rehabilitation Research. J Orthop Sport Phys 39:287–295.

Neuper C, Wörtz M, Pfurtscheller G (2006) ERD/ERS patterns reflecting sensorimotor activation and deactivation. In: ERD/ERS patterns reflecting sensorimotor activation and deactivation, pp 211–222 Progress in Brain Research. Elsevier.

Newell KM (1991) Motor Skill Acquisition. Annu Rev Psychol 42:213–237.

Nudo RJ, Milliken GW, Jenkins WM, Merzenich MM (1996) Use-dependent alterations of movement representations in primary motor cortex of adult squirrel monkeys. J Neurosci 16:785–807.

Nyberg L, Eriksson J, Larsson A, Marklund P (2006) Learning by doing versus learning by thinking: An fMRI study of motor and mental training. Neuropsychologia 44:711–717.

Nyberg L, McIntosh AR, Cabeza R, Habib R, Houle S, Tulving E (1996) General and specific brain regions involved in encoding and retrieval of events: what, where, and when. Proc Natl Acad Sci USA 93:11280–11285.

Oldfield RC (1971) The assessment and analysis of handedness: The Edinburgh inventory. Neuropsychologia 9:97–113.

Olsson C-J (2008) Learning by doing and learning by thinking: An fMRI study of combining motor and mental training. Front Hum Neurosci 2:5.

Olsson C-J, Jonsson B, Larsson A, Nyberg L (2008) Motor Representations and Practice Affect Brain Systems Underlying Imagery: An fMRI Study of Internal Imagery in Novices and Active High Jumpers. Open Neuroimaging J 2:5–13.

Olsson C-J, Nyberg L (2010) Motor imagery: if you can"t do it, you won"t think it. Scandinavian Journal of Medicine & Science in Sports 20:711–715.

Ono T, Kimura A, Ushiba J (2013) Daily training with realistic visual feedback improves reproducibility of event-related desynchronisation following hand motor imagery. Clinical Neurophysiology 124:1779–1786.

Oostra KM, Van Bladel A, Vanhoonacker ACL, Vingerhoets G (2016) Damage to Fronto-Parietal Networks Impairs Motor Imagery Ability after Stroke: A Voxel-Based Lesion Symptom Mapping Study. Front Behav Neurosci 10:9788.

O'Shea H, Moran A (2017) Does Motor Simulation Theory Explain the Cognitive Mechanisms Underlying Motor Imagery? A Critical Review. Front Hum Neurosci 11:189.

Padoa-Schioppa C, Li C-SR, Bizzi E (2002) Neuronal Correlates of Kinematics-to-Dynamics Transformation in the Supplementary Motor Area. Neuron 36:751–765.

Padoa-Schioppa C, Li C-SR, Bizzi E (2004) Neuronal Activity in the Supplementary Motor Area of Monkeys Adapting to a New Dynamic Environment. J Neurophysiol 91:449–473.

Page SJ, Boe S, Levine P (2013) What are the "ingredients" of modified constraint-induced therapy? An evidence-based review, recipe, and recommendations. Restorative neurology and neuroscience 31:299–309.

Page SJ, Dunning K, Hermann V, Leonard A, Levine P (2011) Longer versus shorter mental practice sessions for affected upper extremity movement after stroke: a randomized controlled trial. Clin Rehabil 25:627–637.

Page SJ, Levine P, Leonard A (2007) Mental Practice in Chronic Stroke. Stroke 38:1293–1297.

Pascual-Leone A, Grafman J, Hallett M (1994) Modulation of cortical motor output maps during development of implicit and explicit knowledge. Science 263:1287–1289.

Penhune VB, Doyon J (2002) Dynamic Cortical and Subcortical Networks in Learning and Delayed Recall of Timed Motor Sequences. J Neurosci 22:1397–1406.

Percio CD, Infarinato F, Iacoboni M, Marzano N, Soricelli A, Aschieri P, Eusebi F, Babiloni C (2010) Movement-related desynchronization of alpha rhythms is lower in athletes than non-athletes: A high-resolution EEG study. Clinical Neurophysiology 121:482–491.

Peters HT, Page SJ (2015) Integrating Mental Practice with Task-specific Training and Behavioral Supports in Poststroke Rehabilitation. Physical Medicine and Rehabilitation Clinics of North America 26:715–727.

Petersen SE, van Mier H, Fiez JA, Raichle ME (1998) The effects of practice on the functional anatomy of task performance. Proc Natl Acad Sci USA 95:853–860.

Pfurtscheller G (2001) Functional brain imaging based on ERD/ERS. Vision Research 41:1257–1260.

Pfurtscheller G, Lopes da Silva FH (1999) Event-related EEG/MEG synchronization and desynchronization: basic principles. Clinical Neurophysiology 110:1842–1857.

Pfurtscheller G, Neuper C (1997) Motor imagery activates primary sensorimotor area in humans. Neuroscience Letters 239:65–68.

Pilacinski A, Wallscheid M, Lindner A (2018) Human posterior parietal and dorsal premotor cortex encode the visual properties of an upcoming action Marinovic W, ed. PLoS ONE 13:e0198051.

Poldrack RA (2005) The Neural Correlates of Motor Skill Automaticity. J Neurosci 25:5356–5364.

Popa LS, Ebner TJ (2019) Cerebellum, Predictions and Errors. Front Cell Neurosci 12:375.

Popa LS, Hewitt AL, Ebner TJ (2012) Predictive and Feedback Performance Errors Are Signaled in the Simple Spike Discharge of Individual Purkinje Cells. J Neurosci 32:15345–15358.

Popa LS, Hewitt AL, Ebner TJ (2013) Purkinje Cell Simple Spike Discharge Encodes Error Signals Consistent with a Forward Internal Model. Cerebellum 12:331–333.

Porro CA, Francescato MP, Cettolo V, Diamond ME, Baraldi P, Zuiani C, Bazzocchi M, di Prampero PE (1996) Primary Motor and Sensory Cortex Activation during Motor Performance and Motor Imagery: A Functional Magnetic Resonance Imaging Study. J Neurosci 16:7688–7698.

Ptak R, Schnider A, Fellrath J (2017) The Dorsal Frontoparietal Network: A Core System for Emulated Action. Trends Cogn Sci (Regul Ed) 21:589–599.

Querfurth S, Schücker L, de Lussanet MHE, Zentgraf K (2016) An Internal Focus Leads to Longer Quiet Eye Durations in Novice Dart Players. Front Psychol 7:6.

Riccio I, Iolascon G, Barillari MR, Gimigliano R, Gimigliano F (2010) Mental practice is effective in upper limb recovery after stroke: a randomized single-blind cross-over study. European journal of physical and rehabilitation medicine 46:19–25.

Rieger M, Massen C (2013) Tool characteristics in imagery of tool actions. Psychological Res 78:10–17.

Rienhoff R, Hopwood MJ, Fischer L, Strauss B, Baker J, Schorer J (2013) Transfer of motor and perceptual skills from basketball to darts. Front Psychol 4:593.

Rizzolatti G, Cattaneo L, Fabbri-Destro M, Rozzi S (2014) Cortical Mechanisms Underlying the Organization of Goal-Directed Actions and Mirror Neuron-Based Action Understanding. Physiol Rev 94:655–706.

Rizzolatti G, Luppino G, Matelli M (1998) The organization of the cortical motor system: new concepts. Electroencephalography and Clinical Neurophysiology 106:283–296.

Rizzolatti G, Matelli M (2003) Two different streams form the dorsal visual system: anatomy and functions. Exp Brain Res 153:146–157.

Roland PE, Larsen B, Lassen NA, Skinhoj E (1980) Supplementary motor area and other cortical areas in organization of voluntary movements in man. J Neurophysiol 43:118–136.

Rosenthal CR, Kennard C, Soto D (2010) Visuospatial Sequence Learning without Seeing Robertson E, ed. PLoS ONE 5:e11906.

Ross JS, Tkach J, Ruggieri PM, Lieber M, Lapresto E (2003) The mind's eye: functional MR imaging evaluation of golf motor imagery. AJNR American journal of neuroradiology 24:1036–1044.

Rubinov M, Sporns O (2010) Complex network measures of brain connectivity: Uses and interpretations. NeuroImage 52:1059–1069.

Ruffino C, Papaxanthis C, Lebon F (2017) Neural plasticity during motor learning with motor imagery practice: Review and perspectives. Neuroscience 341:61–78.

Rushworth M (1997) The left parietal cortex and motor attention. Neuropsychologia 35:1261–1273.

Rushworth MFS, Krams M, Passingham RE (2001) The Attentional Role of the Left Parietal Cortex: The Distinct Lateralization and Localization of Motor Attention in the Human Brain. Journal of Cognitive Neuroscience 13:698–710.

Schack T (2004) The cognitive architecture of complex movement. International Journal of Sport and Exercise Psychology 2:403–438.

Schack T, Mechsner F (2006) Representation of motor skills in human long-term memory. Neuroscience Letters 391:77–81.

Schnitzler A, Gross J (2005) Functional Connectivity Analysis in Magnetoencephalography. In: Functional Connectivity Analysis in Magnetoencephalography, pp 173–195 International Review of Neurobiology. Elsevier.

Schoffelen JM, Gross J (2009) Source connectivity analysis with MEG and EEG Salmelin R, Baillet S, eds. Human Brain Mapping 30:1857–1865.

Schorer J, Jaitner T, Wollny R, Fath F, Baker J (2012) Influence of varying focus of attention conditions on dart throwing performance in experts and novices. Exp Brain Res 217:287–297.

Schuster C, Hilfiker R, Amft O, Scheidhauer A, Andrews B, Butler J, Kischka U, Ettlin T (2011) Best practice for motor imagery: a systematic literature review on motor imagery training elements in five different disciplines. BMC Med 9:25.

Seitz RJ, Canavan AGM, Yagüez L, Herzog H, Teilmann L, Knorr U, Huang Y, Hömberg V (1994) Successive roles of the cerebellum and premotor cortices in trajectorial learning. Neuroreport 5:2541–2544.

Seitz RJ, Roland PE, Bohm C, Greitz T, Stone-Elander S (1990) Motor learning in man. Neuroreport 1:57–60.

Shadmehr R (2018) Motor Learning: A Cortical System for Adaptive Motor Control. Current Biology 28:R793–R795.

Shadmehr R, Smith MA, Krakauer JW (2010) Error Correction, Sensory Prediction, and Adaptation in Motor Control. Annu Rev Neurosci 33:89–108.

Sherwood DE, Lohse KR, Healy AF (2014) Judging joint angles and movement outcome: Shifting the focus of attention in dart-throwing. J Exp Psychology Hum Percept Perform 40:1903–1914.

Shmuelof L, Yang J, Caffo B, Mazzoni P, Krakauer JW (2014) The neural correlates of learned motor acuity. J Neurophysiol 112:971–980.

Sirigu A, Duhamel JR, Cohen L, Pillon B, Dubois B, Agid Y (1996) The Mental Representation of Hand Movements After Parietal Cortex Damage. Science 273:1564–1568.

Smeets JBJ, Frens MA, Brenner E (2002) Throwing darts: timing is not the limiting factor. Exp Brain Res 144:268–274.

Smith D, Wright CJ, Cantwell C (2008) Beating the Bunker. Res Q Exerc Sport 79:385–391.

Smith SM (2002) Fast robust automated brain extraction. Hum Brain Mapp 17:143–155.

Smith SM, Jenkinson M, Woolrich MW, Beckmann CF, Behrens TEJ, Johansen-Berg H, Bannister PR, De Luca M, Drobnjak I, Flitney DE, Niazy RK, Saunders J, Vickers J, Zhang Y, De Stefano N, Brady JM, Matthews PM (2004) Advances in functional and structural MR image analysis and implementation as FSL. NeuroImage 23:S208–S219.

Solodkin A, Hlustik P, Chen EE, Small SL (2004) Fine Modulation in Network Activation during Motor Execution and Motor Imagery. Cereb Cortex 14:1246–1255.

Solomon JP, Kraeutner SN, Bardouille T, Boe SG (*under review - BRES-D-18-01445_R2*) Probing the temporal dynamics of movement inhibition in motor imagery.

Solopchuk O, Alamia A, Dricot L, Duque J, Zénon A (2017) cTBS disruption of the supplementary motor area perturbs cortical sequence representation but not behavioural performance. NeuroImage 163:34–40.

Spittle M, Kremer P (2010) Mental Practice and the Retention of Motor Learning: A Pilot Study. Percept Mot Skills 110:888–896.

Steel A, Song S, Bageac D, Knutson KM, Keisler A, Saad ZS, Gotts SJ, Wassermann EM, Wilkinson L (2016) Shifts in connectivity during procedural learning after motor cortex stimulation: A combined transcranial magnetic stimulation/functional magnetic resonance imaging study. Cortex 74:134–148.

Sun FT, Miller LM, D'Esposito M (2004) Measuring interregional functional connectivity using coherence and partial coherence analyses of fMRI data. NeuroImage 21:647–658.

Sun FT, Miller LM, Rao AA, D'Esposito M (2006) Functional Connectivity of Cortical Networks Involved in Bimanual Motor Sequence Learning. Cereb Cortex 17:1227–1234.

Sutton BP, Ouyang C, Karampinos DC, Miller GA (2009) Current trends and challenges in MRI acquisitions to investigate brain function. International Journal of Psychophysiology 73:33–42.

Tanji J, Kurata K (1982) Comparison of movement-related activity in two cortical motor areas of primates. J Neurophysiol 48:633–653.

Tanji J, Shima K (1994) Role for supplementary motor area cells in planning several movements ahead. Nature 371:413–416.

Tanji J, Shima K (2004) Supplementary Motor Cortex in Organization of Movement. Eur Neurol 36:13–19.

Taylor JA, Ivry RB (2012) The role of strategies in motor learning. Annals of the New York Academy of Sciences 1251:1–12.

Tian X (2010) Mental imagery of speech and movement implicates the dynamics of internal forward models. Front Psychol 1:166.

Todorov E, Shadmehr R, Bizzi E (2010) Augmented Feedback Presented in a Virtual Environment Accelerates Learning of a Difficult Motor Task. J Motor Behav 29:147–158.

Tyč F, Boyadjian A (2011) Plasticity of motor cortex induced by coordination and training. Clinical Neurophysiology 122:153–162.

undefined (2006) Kinesthetic, but not visual, motor imagery modulates corticomotor excitability. Exp Brain Res 168.

Ungerleider L (2002) Imaging Brain Plasticity during Motor Skill Learning. Neurobiology of Learning and Memory 78:553–564.

van Beers RJ (2009) Motor Learning Is Optimally Tuned to the Properties of Motor Noise. Neuron 63:406–417.

van Beers RJ, van der Meer Y, Veerman RM (2013) What Autocorrelation Tells Us about Motor Variability: Insights from Dart Throwing Balasubramaniam R, ed. PLoS ONE 8:e64332.

Verwey WB, Shea CH, Wright DL (2014) A cognitive framework for explaining serial processing and sequence execution strategies. Psychon Bull Rev 22:54–77.

Vickers JN (1996) Visual control when aiming at a far target. J Exp Psychology Hum Percept Perform 22:342–354.

Vrba J, Taulu S, Nenonen J, Ahonen A (2009) Signal Space Separation Beamformer. Brain Topogr 23:128–133.

Wakefield C, Smith D, Moran AP, Holmes P (2013) Functional equivalence or behavioural matching? A critical reflection on 15 years of research using the PETTLEP model of motor imagery. International Review of Sport and Exercise Psychology 6:105–121.

Wei G, Luo J (2010) Sport expert's motor imagery: Functional imaging of professional motor skills and simple motor skills. Brain Research 1341:52–62.

Weilke F, Spiegel S, Boecker H, Einsiedel von HG, Conrad B, Schwaiger M, Erhard P (2001) Time-Resolved fMRI of Activation Patterns in M1 and SMA During Complex Voluntary Movement. J Neurophysiol 85:1858–1863.

Weinberg R, Butt J, Knight B, Burke KL, Jackson A (2003) The Relationship Between the Use and Effectiveness of Imagery: An Exploratory Investigation. Journal of Applied Sport Psychology 15:26–40.

Weiss PH, Dohle C, Binkofski F, Schnitzler A, Freund H-J, Hefter H (2001) Motor impairment in patients with parietal lesions: disturbances of meaningless arm movement sequences. Neuropsychologia 39:397–405.

Wohldmann EL, Healy AF, Bourne LE (2007) Pushing the limits of imagination: Mental practice for learning sequences. J Exp Psychol Learn Mem Cogn 33:254–261.

Wolpert DM, Miall RC, Kawato M (1998) Internal models in the cerebellum. Trends Cogn Sci (Regul Ed) 2:338–347.

Woodworth RS, Thorndike EL (1901) The influence of improvement in one mental function upon the efficiency of other functions. (I). Psychological Review 8:247–261.

World Darts Federation (2017): WDF Playing and Tournament Rules July 25, 2017. Available from: URL: http://www.dartswdf.com/rules/.

Wulf G, Horstmann G, Choi B (1995) Does Mental Practice Work like Physical Practice without Information Feedback? Res Q Exerc Sport 66:262–267.

Wulf G, Shea C, Lewthwaite R (2010) Motor skill learning and performance: a review of influential factors. Medical Education 44:75–84.

Wulf G, Shea CH (2002) Principles derived from the study of simple skills do not generalize to complex skill learning. Psychon Bull Rev 9:185–211.

Xu L, Zhang H, Hui M, Long Z, Jin Z, Liu Y, Yao L (2014) Motor execution and motor imagery: A comparison of functional connectivity patterns based on graph theory. Neuroscience 261:184–194.

Yang J (2014) The influence of motor expertise on the brain activity of motor task performance: A meta-analysis of functional magnetic resonance imaging studies. Cognitive Affect Behav Neurosci 15:381–394.

Yarrow K, Brown P, Krakauer JW (2009) Inside the brain of an elite athlete: the neural processes that support high achievement in sports. Nat Rev Neurosci 10:585–596.

Zenon A, Sidibe M, Olivier E (2015) Disrupting the Supplementary Motor Area Makes Physical Effort Appear Less Effortful. J Neurosci 35:8737–8744.

Zentgraf K, Green N, Munzert J, Schack T, Tenenbaum G, Vickers JN, Weigelt M, Wolfensteller U, Heekeren HR (2009) How are actions physically implemented? In: How are actions physically implemented?, pp 303–318 Progress in Brain Research. Elsevier.

Zhang H, Xu L, Wang S, Xie B, Guo J, Long Z, Yao L (2011) Behavioral improvements and brain functional alterations by motor imagery training. Brain Research 1407:38–46.

Zhang H, Xu L, Zhang R, Hui M, Long Z, Zhao X, Yao L (2012) Parallel Alterations of Functional Connectivity during Execution and Imagination after Motor Imagery Learning Wenderoth N, ed. PLoS ONE 7:e36052.

Zhang Q, Zhang P, Song L, Yang Y, Yuan S, Chen Y, Sun S, Bai X (2019) Brain Activation of Elite Race Walkers in Action Observation, Motor Imagery, and Motor Execution Tasks: A Pilot Study. Front Hum Neurosci 13:170.

Zhang T, Liu T, Li F, Li M, Liu D, Zhang R, He H, Li P, Gong J, Luo C, Yao D, Xu P (2016) Structural and functional correlates of motor imagery BCI performance: Insights from the patterns of fronto-parietal attention network. NeuroImage 134:475–485.