

Measuring Mental Imagery

by

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A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

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Abstract

Mental imagery describes the cognitive ability to form internal representations of our sensorimotor experiences. It follows that there are different types of mental imagery, such as visual, auditory, kinesthetic, motor, and spatial. The work presented here sought to further develop and validate a novel objective measure of motor imagery. Specifically, does this novel questionnaire require motor imagery processes for successful completion. If so, the nature of ‘hands’ being the contents of an individual’s movement imagery would suggest that hand-dominance effects could be observed. The first study described in Chapter 1 hypothesized that given a sufficient sample of right-handed participants and trials of both right- and left-hand stimuli, right-handed participants should perform better on right-hand trials than left-hand trials. A pencil-and-paper hand-version of the Test of Ability in Movement Imagery was administered to 79 right-handed participants, and a significant right-handedness effect was observed. Given the results in Chapter 1, a follow-up study utilizing a computerized version of the pencil-and-paper hand-imagery questionnaire was administered to 22 right-handed and 18 left-handed participants, while electroencephalography data was recorded. We hypothesized that mu oscillations, which are suppressed at the onset and duration of both real and simulated action, would produce contralateral event-related desynchronization (suppression) to the hand in which finger movements were being mentally simulated. Further, we expected a handedness effect to also be detected electrophysiologically, such that right-handed participants would display greater mu suppression over electrode site C3 (left cerebral hemisphere), whereas left-handed participants would display greater mu suppression over electrode site C4 (right cerebral hemisphere). Oscillatory analysis depicted a significant increase of frontal-midline theta and posterior alpha power during correct versus error trials. This pattern of results suggests

participants employed spatial working memory to successfully complete the task. Taking the results from the two studies together, insight is gained regarding the factors of experimental design determining the qualities of spatial imagery attended to by participants.

Preface

The research conducted for this thesis received ethics approval from the University of Alberta Research Ethics Board Name 'ZAUB 892' No. 18708, October 25, 2016. The questionnaire used in this work was an adaptation of the original Test of Ability in Movement Imagery, designed by Madan and Singhal (2013). All work appearing here was done by myself, under the supervision of Dr. Anthony Singhal and Dr. Chris Madan.

Chapter 2 of this thesis has been published as Donoff, C.M., Madan, C.R., and Singhal, A., "Handedness effects of imagined fine motor movements", *Laterality*, vol. 23, issue 2, 228-248.

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Chapter 1:

General Introduction

Introduction

The theory of mental imagery attempts to provide an explanation of how we are able to form sensorimotor experiences in the absence of external stimuli or explicit movement. The qualia that is experienced can either be of past events in the form of episodic memory, or of constructed recombinations of experiences never before perceived. Our ability to manipulate and interact with these internally held simulations enables us to perform a wide variety of tasks, including our capacity to plan for the future (Moulton & Kosslyn, 2009; Pearl & Mackenzie, 2018), navigate our surroundings (Bocchi et al., 2017), attend to spatial features and orientation (Palermo et al., 2008), and engage in creativity (Zaidel, 2014). Mental imagery has been invoked to explain decision making processes (Kamleitner, 2011), counterfactual thinking (Barlett & Brannon, 2007), mental rehearsal effects in sport performance (Filgueiras et al., 2018), as well as the emergence of impossible objects (eg. a sculpture of a lion's head on a human's body; Judea & Mackenzie, 2018). Despite the breadth of behaviors and cognitive functions affected by this core process of mental simulation, there has yet to be an all-encompassing explanation as to how it arises.

Mental imagery theories generally fall under either a depictive or descriptive approach. Descriptive approaches advocate for an abstract, language-like process that translates sensorimotor experiences into amodal symbols used to make propositions (Pylyshyn, 2002). Depictive approaches instead posit that the basic sensorimotor processes used to interact with the environment form the very contents for generating more detailed representations or relationships. One depictive theory of mental imagery that has accumulated support from neuroimaging studies is the simulation theory (Davidson & Schwartz, 1977). The simulation theory incorporates the utility of modal representation, and posits that mental imagery arises from the reactivations of

primary sensory and motor regions, and that these form ‘perceptual symbols’ used in higher-order cognitive functions (Farah et al., 1988). Extant studies have observed overlaps in neural activity between mental imagery and perception-based tasks, indicating that these inner representations need not be translated into amodal symbols (O’Craven & Kanwisher, 2000; Kosslyn, Ganis, & Thompson, 2006). Distributed reactivations of sensorimotor regions by the hippocampus during memory retrieval (Eichenbaum, 2012), as well as interference and facilitation effects of visual imagery on subsequent visual detection tasks further supports the notion that mental imagery evokes activity in overlapping sensorimotor regions (Craver-Lemley & Reeves, 1992; Wu et al., 2012). Barsalou (2008) also suggests that there are different types of simulators, some that are automatic (unconscious), and others that are deliberate (conscious). The term ‘mental imagery’ often refers to these deliberate, conscious simulations, however it is important to recognize the influence of our automatic, unconscious simulations. Gibson’s theory of affordances (Gibson, 1977, 1979), which postulates that our perceptual system automatically encodes the functional usefulness of objects in our environment, is an example of automatic simulation. Further, a study by Hardy et al. (2003) depicted the automatic activation of motor cortices when tools versus non-tools were presented. The automatic simulation of both motor and visual information is an example of how mental imagery in general can integrate multiple sensorimotor modalities to model more nuanced relationships. This leads to a discussion on proposed types of mental imagery, and how they can be measured.

Mental imagery can be described by the sensory modality being simulated, such as visual (Palmiero et al., 2009; Dijkstra et al., 2019), auditory (Martin et al., 2018; Pruitt, Halpern, & Pfordresher, 2019), tactile (Olivetti Belardinelli et al., 2004), gustatory (Bensafi et al., 2013), olfactory (Del Gratta et al., 2001), and motor (Callow & Hardy, 2004). In the literature, there has

been a distinction between two forms of visual imagery, both sharing the common capability of forming an mental image in the absence of any external stimulus. Two forms of visual imagery are object and spatial (Blajenkova, Kozhevnikov, & Motes, 2006). Object imagers attend to qualities appearing in pictorial representations, such as color, shape, size, visual complexity, and brightness. Spatial imagers employ a more abstract form of representation, attending to spatial properties between objects or parts of objects, such as distance, relative size, quantity, movement, and location. Further, object imagery entails processing visual information globally, whereas spatial imagery is associated with sequential, analytic inspection, resulting in distinct imagery abilities (Kozhevnikov et al., 2010; Blazhenkova, 2016). The Object Spatial Imagery Questionnaire (OSIQ; Blajenkova, Kozhevnikov, & Motes, 2006) was designed to measure individual differences in preferences and experiences in object and spatial imagery. Principal components analysis of this questionnaire yielded the two expected factors, providing initial construct validity of the task. Further, natural scientists were found to have higher scores on the Spatial scale than artists and professionals in the humanities, whereas artists were found to score higher on the Object Scale compared to scientists or humanities professionals (Blajenkova, Kozhevnikov, & Motes, 2006; Blazhenkova, 2016). Identifying preferences in the form of imagery people default to is important, because going forward, it changes how we instruct people to perform mental imagery if we want certain properties of the imagined percept to be attended to. This questionnaire poses to provide promising insight via its future relations with other extant measures of mental imagery, assisting in the clarification of which forms of imagery are utilized by participants on specific imagery tasks.

There has also been a distinction between two forms of motor imagery, kinesthetic motor imagery (KMI) and visual motor imagery (VMI). KMI requires the imagined motor movement to

include simulations of the sensory feeling associated with a given action in an egocentric (first-person) frame of reference. VMI allows imagery in either an egocentric or allocentric (third-person) frame of reference, involving the self-visualization of a movement (Toriyama, Ushiba, & Ushiyama, 2018). Both KMI and VMI movements can be made in conjunction with tool/object use (transitive), or in the absence of any tools/objects (intransitive). Researchers have demonstrated that left hemisphere parietal and premotor area lesions generally produce apraxia (an inability to form motor plans of movements) (Geschwind, 1965; Hanna-Pladdy et al., 2001; Heilman & Gonzalez Rothi, 2003). This idea was verified in physiological studies of normal praxis performance using EEG (Wheaton et al., 2005), as well as functional magnetic resonance imaging (fMRI) studies demonstrating elicitation of the inferior frontal gyrus (IFG), precentral gyrus (PcG), inferior parietal lobule (IPL), superior parietal lobule (SPL), and supplementary motor area (SMA) during imagined transitive movements (Héту et al., 2013). There have been depictions of differences between the observation of transitive and intransitive movements, with the former more consistently activating posterior parietal (PPC) regions (Balconi & Cortesi, 2016). This is relevant to mental imagery, since observing someone else perform an action utilizes overlapping regions also employed during motor imagery (Orr et al., 2008). For example, motor regions such as the primary motor cortex (M1), premotor cortex (PMC), and supplementary motor area (SMA) were shown to activate during both action observation and motor imagery of gymnastic movements (Munzert et al., 2008). With the previous finding by Balconi and Cortesi (2016) showing increased PPC activity for observed transitive movements, mentally simulating transitive movements may further require the integration of other information such as object manipulation knowledge (Ishibashi et al., 2018). These results introduce the importance of recording brain activity during mental imagery, ensuring the desired

motor movements (transitive or intransitive) and sensorimotor modalities are being mentally simulated.

Investigations of the cortical electrophysiology associated with mental imagery emerged after years of relating mental states with other measurable physiological markers such as the galvanic reflex, heart rate, and muscle-fibre contractions (Beisteiner et al., 1995). To this day, one of the best ways to achieve high temporal resolution when recording brain activity in humans is with electroencephalography (EEG), which measures the summed activity of populations of neurons located in the thin, outer layer of the brain, the cortex. There are several ways of examining the electrical activity produced by the brain. Event-related potentials (ERP) index brain activity that occurs in response to discrete events. When studying endogenously generated mental processes, where the cognitive processes' onset of interest is ambiguous, it is useful to be able to measure more longitudinal fluctuations in activity. In this case, oscillatory analysis is performed, where oscillations constitute neuronal rhythmic activity produced as the result of neurons firing in a temporally synchronized manner (Buszaki, 2006). Analytic methods require the ability to distinguish rhythmic, oscillatory activity from other artefactual activity that can resemble the time-frequency dynamics of neuronal oscillations. Often, Fourier or wavelet transforms of the signal are used to separate signal from noise, however these methods entail assumptions about electrophysiological waveforms that are violated in nature, such as selecting frequencies with the largest spectral peak. Further, there is a high degree of variation between studies in the specific thresholds used to identify oscillatory activity. The Better OSCillation detection method (BOSC; Caplan et al., 2001; Whitten et al., 2010) provides a consistent way to determine thresholds across frequency, electrode (site), task, electrophysiological state, and species. Both a power and duration threshold is determined according to a model of the

background power spectrum. The BOSC method provides a more conservative method, compared to taking autocorrelations of the EEG signal, to ensure the detected rhythmic activity has a high likelihood of originating from desired neuronal sources, without washing out signal using pre-whitening techniques (normalizing power across frequency). Like ERP components, rhythmic activity within specific frequency bands has been correlated with different aspects of behavior, and two rhythms, mu and theta, are of particular interest for the work presented in the following chapters.

The mu rhythm, which occupies the same frequency band as posterior alpha (8-13 Hz), represents oscillatory activity involved in sensorimotor function occurring over the motor cortex (Nam et al., 2011). In direct opposition to what we expect of theta, mu activity is present during periods of stillness and desynchronizes at the onset of an overt or imagined movement (Pfurtscheller et al., 2006). Consistent with this, Pfurtscheller and Neuper (1997) reported increased mu power in the motor cortical region for hand movements during foot movement, for which activation of the hand area is unnecessary. There have been other depictions of mu event-related desynchronization (ERD) associated with imagined gross-body and hand movements (Pfurtscheller et al., 2006; Nam et al., 2011). One example comes from Llanos and others (2013), where they observed greater mu suppression after visual stimuli that initiated motor planning versus passive observation. Specifically, participants were presented with a visual stimulus (an arrow) which primed motor planning (which can be executed or imagined later after the display of a second stimulus). The observation that mu suppression was similar during motor testing and imagery testing supports the idea that the similar cortical mechanisms are recruited during the planning of real and simulated movements.

The cortical theta rhythm, occupying the 4 – 7 Hz frequency band, is typically found over the frontal-midline region of the scalp. This frontal-midline theta is thought to assist in mental functions requiring high levels of attention and effort, which imagery tasks involve (Brookings et al., 1996). For example, Valadez and Simons (2018) determined a relationship between frontal midline theta and the degree of post-error slowing during a flanker task. In this paradigm, subjects were presented with horizontal strings of letters, with congruent (i.e., ‘MMMMM’) or incongruent (i.e., ‘NNMNN’) trials., with participants instructed to identify the middle letter. Results depicted that greater frontal-midline theta is not related to greater post-error slowing. Rather, during successful error recovery (i.e., when an error response is followed by a correct response) greater frontal-midline theta power is associated with less slowing, indicating that frontal-midline theta activity may in part serve cognitive control by influencing the rate of information accumulation. If theta serves this function of identifying correctly encoded information, it may play a role in objective measures of mental imagery. As well, frontal-midline theta has been reported in air traffic controllers during simulated air traffic control tasks (Shou & Ding, 2013), with higher difficulty situations resulting in increased frontal midline theta (Brookings et al., 1996). Further, Cruikshank and others (2012) measured oscillatory EEG activity during visually-guided and delayed goal-directed reaching. Frontal-midline theta oscillations were detected during movement initiation and execution, and were significantly more prevalent at temporal sites in delayed versus visually-guided reaching during action-planning. This observation further suggests that frontal-midline theta synchronization may represent a means to improve cognitive control. Taken together, these results indicate that variables such as task difficulty, or the necessity of keeping multiple elements in working memory, have an effect on the degree of frontal-midline theta synchronization observed. It is

possible that when imagining complex actions or visuospatial representations, greater cognitive control is required to hold an image in mind and manipulate features of this representation (such as form, relative position, location, etc.). It becomes apparent that careful consideration is required when selecting or designing imagery paradigms to ensure desired forms of imagery are being elicited.

The type of imagery questionnaire or test can influence both the form of imagery employed by the participant, as well as measure different facets of mental imagery ability, such as vividness, preference, and control. There are both subjective and objective measures of mental imagery. Subjective measures use self-report questionnaires, requiring participants to reflect on different qualities of their imagery experience. In extant studies, imagery vividness has been defined in different ways. Sometimes increased vividness is described as more closely approximating the real percept, and at other times the emphasis is purely on how immersed the individual felt (McAvinue & Robertson, 2006). As we understand the multi-faceted nature of mental imagery, it becomes apparent how important clear and concise nomenclature is to ensure experimenters are inducing and measuring the desired mental imagery. There are a number of questionnaires available to measure imagery vividness, many using a Likert-scale to record participant responses. There have been efforts to relate these subjective questionnaires to other cognitive tasks of learning, memory, and perception, which are thought to involve imagery. With much of the extant literature finding inconsistent results, it has led some to the conclusion that these questionnaires possess poor predictive validity (Kaufmann, 1981; Schwitzgebel, 2002). Any inconsistencies in the correlations found between imagery questionnaires and cognitive tasks involving imagery could be due to differences in the specific abilities measured by the questionnaires themselves (McAvinue & Robertson, 2006). For example, the Questionnaire

Upon Mental Imagery (QMI; Betts, 1909) measures the vividness of imagery in seven sensory modalities, and it may not be appropriate to relate this questionnaire with another task that only measures a specific modality. Objective tests of mental imagery provide tasks that require imagery processes for their solution. A common type of objective test measures an individual's ability to form and manipulate visuospatial representations. For example, the Revised Minnesota Paper Form Board (Likert & Quasha, 1937) task requires participants to mentally fit together separated pieces to form a holistic figure, requiring the mental formation and manipulation of spatial properties. Importantly, participants can either successfully or unsuccessfully complete objective tasks, providing an index of general imagery ability. However, the output of objective tasks does not directly measure an individual's ability to attend to specific aspects of their imagery experience. Rather, the measure obtains a more holistic depiction of an individual's ability, in which it is uncertain the degree to which a participant imagines particular qualities of the phenomenon to successfully perform the task. With there being a set of spatial abilities (such as spatial transformations, assessments of relative position, object form, etc.), it is prudent to be concise in the conclusions one draws from imagery tasks utilizing an objective measure (Kosslyn et al., 2004).

The following chapters contain two studies attempting to further validate and develop a novel objective test of mental imagery. The desire to improve objective measures of mental imagery has several motivations. First, being able to obtain an index of imagery ability beyond that which can be self-identified by a participant is paramount, as there are automatic imagery processes that researchers may be interested in, such as the simulation of object function information while navigating an environment. Further, subjective questionnaires introduce the potential for diverging interpretations of what is meant by constructs such as 'vividness'.

Performance-based measures of mental imagery provide an implicit way of elucidating aspects of imagery that subjects may not be able to identify via self-report, making them a valuable tool in future investigations of mental imagery.

Chapter 2:
Handedness Effects of Imagined Fine Motor Movements

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Abstract

Previous studies of movement imagery have found inter-individual differences in ability to imagine whole-body movements. The majority of these studies have used subjective scales to measure imagery ability, which may be confounded by other factors related to effort. Madan and Singhal (2013) developed the Test of Ability in Movement Imagery (TAMI) to address these confounds by using a multiple-choice format with objectively correct responses. Here we developed a novel movement imagery questionnaire targeted at assessing movement imagery of fine-motor hand movements. This questionnaire included two sub-scales: functionally-involved (i.e., tool-related) and isolated (i.e., hand-only). Hand dominance effects were observed, such that right-handed participants were significantly better at responding to right-hand questions compared to left-hand questions for both sub-scales. A stronger handedness effect was observed for functionally-involved movement imagery, and it did not correlate with the Edinburgh Handedness Inventory. We propose that the functionally-involved imagery subscale provides an objective hand imagery test that induces egocentric spatial processing and a greater involvement of memory processes, potentially providing a better skill-based measure of handedness.

Keywords: movement imagery; handedness; imagery; tool use; objects

Drs. Anthony Singhal, Chris R. Madan, and Mr. Christopher M. Donoff have no conflicts of interest or financial ties to disclose.

Introduction

Mental imagery is broadly defined as the capacity to simulate both sensory processes and motor activity. There are many types of mental imagery, one being designated to the simulation of motoric action, called motor imagery. Motor imagery is distinct from the more common visual imagery – the ability to mentally simulate a single object or scene – both in terms of the frame of reference employed, as well as the use of motion. Specifically, motor imagery typically utilizes an egocentric frame of reference, and has been argued to enhance the degree of kinesthetic feedback (Epstein 1980; Jeannerod 1994; Madan & Singhal 2012; Sirigu & Duhamel 2001). When considering novel ways to measure motor imagery, it is important to first identify the types of movements one is interested in.

Explicit movements can be classified as being either transitive or intransitive. Transitive movements involve the use of objects or tools to achieve particular goals (e.g., using a wrench), whereas intransitive movements are carried out in the absence of object- or tool-use (e.g., waving hand back-and-forth). It has been shown that manual asymmetries exist for tool-use, with right-handed participants performing better for right versus left transitive-limb gestures (Heath et al. 2002). Hand dominance describes the degree to which an individual prefers using their right or left hand when accomplishing typical motor actions (e.g., using a pen, scissors, or spoon). These effects occur because of the functional lateralization of various cognitive processes, including motoric action. Studies have shown that children who are more right-hand dominant perform better on indices of executive function (Mills et al. 2015). The effects of hand dominance also is related to language, as there is evidence suggesting an individual's hand preference correlates with their hemispheric lateralization of language processing (Knecht et al. 2000; Pujol et al. 1999). Further, there have been observations of increased activity in lateralized motor regions

during language processing for hand-related verbs or functionally manipulable nouns, suggesting such abstract cognitive functions as language may be grounded by constructs of mental simulation such as motoric action and hand dominance (Willems et al. 2011; Just et al. 2010; Rueschemeyer et al. 2010; Saccuman et al. 2006). In the current study, observing greater performance by right-handed participants for right-hand stimuli compared to left-hand stimuli would support these proposed relationships between hand dominance and lateralized increases in cognitive function. To validate these relationships, we measured the correlation between laterality scores, operationalized as the difference between right- and left-hand performance, with the Laterality Quotient (LQ) of the Edinburgh Handedness Inventory (EHI) (Oldfield 1971). The EHI is a well-established questionnaire for evaluating handedness. When relating the novel imagery questionnaire's laterality difference score to the LQ of the EHI, we expected to obtain a moderate to strong correlation due to the unifying focus on objects.

Our ability to recognize and prioritize highly manipulable objects depends on our access to previous knowledge and experiences. One way these representations may be retrieved is by movement imagery. It has been suggested that movement imagery can be evoked automatically, without conscious intent. This has been demonstrated by activations of premotor cortex while participants only viewed images or words of functional objects, as opposed to other stimuli (Chao & Martin 2000; Buccino et al. 2001; Jarvelainen et al. 2004; Just et al. 2010; Madan et al. 2016; Yang & Shu 2013). Such automatic activations of movement imagery support the processing of tool-related stimuli and movement imagery's function in higher-level cognition. In the current study, we set out to determine if imagined hand movements can generalize from the handedness effect observed for explicit transitive movements. We developed a novel movement imagery questionnaire to include two types of hand-related movements: functionally-involved

movement and isolated movement. Functionally-involved movements require the participant to imagine transitive hand movements interacting with objects, whereas isolated movements promote the imagining of intransitive hand movements that do not lead to object or tool use. Where other objective tests of movement imagery have focused on whole body and gross limb movements, the novel hand imagery questionnaire provides the ability to measure imagined hand movements specifically, enabling tests to see if hand-dominance predicts movement imagery performance for Isolated-movement and Functionally-involved imagery.

Methods

Participants

A total of 79 right-handed undergraduate students with the average age of 19.14 ($SD = 1.74$) participated for partial credit towards an introductory undergraduate psychology course. All participants provided written consent and the research protocol was approved with the consent of the University of Alberta research ethics board.

Along with obtaining the degree of the student's handedness score using the Edinburgh Handedness Inventory [$M (SD) LQ = 78.69 (16.09)$] (Oldfield, 1971), object experience was recorded. Participants rated each object on a 9-point Likert-scale from low experience (1) to high proficiency (9). Of the 79 individuals who participated, 70 subjects were used in data analysis (49 female), with seven students excluded in all analysis due having a LQ less than 50 (not right-handed), and two excluded due to a lack of compliance with instructions. One student was excluded only from the object experience/performance analyses due to incomplete responses.

Objective movement imagery questionnaires

Many movement imagery questionnaires rely on a participant's subjective self-report of the vividness of their imagery. Although this technique can be useful in conjunction with other imagery questionnaires, it is confounded by inflated confidence or social desirability bias, especially when comparing specific populations such as athletes. The introduction of objective imagery tests, such as the Test of Ability in Movement Imagery (TAMI), addressed this problem by using a multiple-choice format to explicitly test for an individual's imagery ability (Madan & Singhal 2013, 2014). Where TAMI presented whole-body images, the present study used images of hands, and images of highly manipulable objects under the Functionally-involved questions. We related these subscales to the Florida Praxis Imagery Questionnaire (FPIQ) (Ochipa et al. 1997), the original TAMI, as well as the EHI to assess how our novel questionnaire relates to extant measures of movement imagery. The FPIQ has four subscales: kinesthetic, position, action, and object. We predicted that isolated movement imagery should correlate strongly with the position, kinesthetic, and action subscales, however we do not expect a high correlation with the object subscale. Functionally-involved movement imagery should correlate greatest with the object and position subscales of the FPIQ, as the position subscale requires one to imagine their relative finger positions when using different objects, and the object subscale requires an adequate degree of previous experience with the objects. Functionally-involved movement imagery should also correlate to a lesser degree with the kinesthetic and action subscales, since imagining the initial hand shape still requires an ability to imagine finger joint movements. We also predicted a high correlation between isolated movement imagery and whole-body movements from TAMI, since both are not object-oriented, and thus a low correlation is predicted between functionally-involved movement imagery and TAMI.

Materials

Novel Hand Imagery Questionnaire

Our questionnaire provided an objective test of movement imagery focused on hand-related movements. Each question began with an image of an open hand, to depict the initial starting position. Five simple instructions followed, in which the participant was required to read and mentally construct the final hand position. An example of the five finger-movement instructions is as follows: “1. Lay your hand open, palm up, with your fingers together. 2. Spread your fingers apart. 3. Cross your pinky finger in front of your ring finger. 4. Point your middle finger perpendicular to the palm. 5. Touch the tip of your thumb midway up your middle finger.” The full questionnaire along with the instructions participants were provided with can be found in the Appendix. While reading these five instructions, each participant held a tennis ball in the corresponding hand in question to prevent overt hand movements from occurring. Holding the tennis ball kept the hand in a uniform, natural position, acting to prevent any motor commands involved in maintaining an unnatural hand position from arising. Such subtle attention and unconscious planning required to keep the hand in an unnatural position, such as flat against a table, could interfere with an individual’s ability to imagine movements.

The hand imagery questionnaire contained 44 questions, and used a 2 x 2 x 2 design of the between-subject factor Perspective (first-person view, uninstructed), and the within-subject factors Laterality (Right, Left) and Movement Type (Functionally-involved Movement, Isolated Movement). The questionnaire was divided into four booklets: two tested the imagined movements of the right hand, and the other two tested the imagined movements of the left hand. All four booklets contained both movement types. Participants completed the battery of questionnaires in a classroom setting, seated at a desk. The order in which participants completed

the four booklets changed across experimental session to control for order effects, and egocentric perspective instruction was manipulated between experimental sessions.

Isolated hand movement imagery questions required the participant to recognize and select the correct final hand shape in a multiple-choice format (Figure 1A). Hand articulations were constructed by first generating a bank of possible movement instructions, followed by assembling subsets of these instructions in ways that led to distinct hand shapes. All hand images were produced by taking multiple photos of real hands in the selected articulations. Using Adobe Photoshop CS6 (Adobe Systems Inc.; San Jose, CA), photos were then converted to line drawings and scaled to a consistent size.

Functionally-involved movement imagery questions required the participant to judge which of the presented objects they would most likely use with their imagined hand shape (Figure 1B). To see whether functionally-involved movement imagery differentiates from isolated hand movement imagery, we first selected 27 line drawings of highly manipulable objects from the Bank of Standardized Stimuli (BOSS) (Brodeur et al. 2010, 2014; Guérard et al., 2015). The BOSS is a dataset of photos and line drawings of objects that have been normed across a number of dimensions including manipulability. From the 274 line drawings included in version 2.0 of the BOSS, we selected objects based on several criteria: primarily ensuring that each object required a unique hand shape, while also selecting objects with high manipulability scores. In addition to the normed dimension of manipulability, we also considered how familiar participants were with each object, the degree of detailed lines each object possessed (visual complexity), as well as the congruency between the object stimuli and the participants' mental image (object agreement). For our chosen items, the mean (SD) scores of these normed dimensions, where 1 corresponded to low and 5 corresponded to high, were as follows:

$M_{\text{Manipulability}} = 3.23 (.723)$, $M_{\text{Familiarity}} = 4.14 (.467)$, $M_{\text{VisualComplexity}} = 2.35 (.471)$, and $M_{\text{ObjectAgreement}} = 4.14 (.478)$. Mirrored images of objects were incorporated to enhance the congruency between object orientation and mental simulations of either the left or right hand. No object was keyed as the correct answer more than once.

Object experience questionnaire

The object experience questionnaire required participants to self-assess how much experience they had using each of the 27 objects appearing in the functionally-involved movement imagery sub-scale. Assessments were made using a 9-point Likert-scale, where 1 indicated no experience, and 9 indicated very high proficiency. Participants were provided with the same line-drawn images that appear in the right-hand, functionally-involved imagery questions.

Test of Ability in Movement Imagery (TAMI)

The TAMI is a movement imagery questionnaire comprised of 10 questions that assess an individual's ability to imagine whole body movements, including manipulations of the head, arms, torso, and legs (Madan & Singhal, 2013). Questions begin with a set of 5 instructions, each describing a single body movement, with the first instruction fixed across questions to re-orient the participant, for example: "1. Stand up straight with your feet together and your hands at your sides. (See image.) 2. Place both of your hands on top of your head. 3. Step your left foot 30 cm to the side. 4. Turn your torso 60° to the right. 5. Tilt your head downward, towards your chest." Following are 5 line drawings of final body positions for the participant to choose from, as well as options for "None" and "Unclear". Answers designed to be decoys differed by a

minimum of two movements. See Figure 1 of Madan and Singhal (2015) for an example. Participants were instructed to imagine the movements as their own, and to refrain from moving in any way. A practice question was provided with immediate feedback, as well as an opportunity to flip back and reread the instructions. We used the alternate scoring method (TAMIw), which reduced ceiling effects by assigning more weight to the more difficult questions, making the test out of 24 points (Madan & Singhal, 2014).

Florida Praxis Imagery Questionnaire (FPIQ)

The FPIQ is a clinical tool used to assess mental imagery ability in patients with apraxia and other movement disorders (Ochipa et al. 1997). Four subscales (position, kinesthetic, object, and action) comprise the FPIQ, each out of 12 points. The position subscale requires the participant to imagine the spatial position of their hand in relation to either an object or their other body parts during some action. For example, “Imagine you are using a fingernail clipper. Which is bent, the index finger or the thumb?” The kinesthetic subscale requires the participant to judge which joint moves the most in a given action. For example, “Imagine you are using an ice pick. Which joint moves more, your elbow or your wrist?” The object subscale requires the subject to make judgments based off of different parameters. For example, “Which is wider, the eraser at the end of a pencil, or the point?” Lastly, the action subscale requires the participant to imagine the motion of a limb when performing an action. For example, “Imagine you are using a handsaw. Does your hand move up and down, or front to back?”

Edinburgh Handedness Inventory (EHI)

The EHI was developed by Oldfield (1971) and is a 10-item questionnaire designed to measure handedness. Participants indicate whether they would prefer to complete a task using their right, left, or either hand by placing checkmarks in either hand column, or both. Further, if there is a hand preference, the strength of this preference is indicated by placing either one or two checkmarks in the respective hand column, where two checkmarks indicate the participant would never use the other hand unless forced to. The Laterality Quotient (LQ) here was calculated as the sum of the number of right-hand checkmarks, divided by the total number of checkmarks provided, and multiplied by 100, resulting in a percentage of right-handedness. The 10 items were: writing, drawing, throwing, scissors, toothbrush, knife (without fork), spoon, broom, striking a match (match), and opening a box (lid).

Procedure

All participants completed the questionnaires in the following fixed order: novel hand imagery questionnaire, TAMI, FPIQ, EHI, and object experience questionnaire.

Prior to beginning the hand imagery questionnaire, participants were given an initial instruction package containing a between-subject manipulation of frame of reference. Half of the participants were explicitly asked to imagine the movement instructions from a first-person perspective (FPV), while the other half were not given an explicit perspective instruction (uninstructed). Examples of either pointing your thumb “*parallel*” or “*perpendicular to the plane of your palm*” were provided to reduce potential confounds due to participants misunderstanding the instructions. The instructions emphasized the importance of holding the tennis ball while reading each question’s movement instructions, in an attempt to prevent any overt movements. If

the experimenter noticed that the participants were not holding the tennis ball while reading the movement instructions, they were reminded to do so.

After completing all imagery questionnaires, participants were given the object experience questionnaire asking them to rate their familiarity with each object from the FM subscale.

Data Analyses

Statistical analyses

A three-way mixed ANOVA was conducted to compare movement imagery accuracy as a function of the between-subject factor Perspective (FPV, uninstructed), and the within-subject factors Laterality (Right-Hand, Left-Hand), and Movement Type (Isolated Movement, Functionally-involved). Correlations were calculated between the accuracy of the movement types and the other imagery questionnaires (TAMIw, FPIQ). Laterality difference scores were obtained by subtracting the Left-Hand accuracy from the Right-Hand accuracy, within each movement type, and then correlated with the EHI.

Functionally-involved movement imagery

To ensure the questions were reasonably difficult, each functionally-involved movement imagery question included objects that involved closely related interactions to prevent the detection of obvious distractors. Questions were designed such that there was always one object that would be more intuitive and natural for the participant, however it is possible that these fit our own judgments, and may not represent the majority's preferences. To address this, we used participants' performance to re-calibrate the scoring of the functionally-involved imagery

questions, as well as eliminate ambiguous questions. First we calculated the proportion of selected responses for each question. This indicated whether responses for a question were relatively consistent across participants or distributed across several options. To establish which questions had low variability in response (i.e., high consistency), versus an even distribution of selection (i.e., ambiguous), a root-mean-squared-deviation (RMSD) score was obtained using questions with scores near 0 representing low consistency and larger RMSD scores denoting high consistency.

To methodically determine where a cutoff point should be for the removal of poor questions, we used an Ordering Points to Identify the Clustering Structure (OPTICS) clustering algorithm (Ankerst et al. 1999; Daszykowski et al. 2002), similar to the approach used by Madan and Singhal (2014). Briefly, RMSD scores were sorted from largest to smallest, and the differences were calculated between adjacent scores. Large differences indicated a wide gap in the consistency for a question. Based on this gap, the lower bound RMSD score and all questions with lower RMSD scores were removed (7 questions). Additionally, because some questions were found to have two high occurrence responses, we divided the remaining questions into those that had only one correct answer, worth 1 point, and others with two correct answers, worth half a point. To do so, we calculated again using a clustering approach. Large difference scores represented questions in which one answer was highly favored, whereas low differences corresponded to questions in which the two most chosen responses had similar selection rates. Based on the cluster analysis, 11 questions were assigned to have one correct answer, and 4 questions assigned to have 2 correct answers (each worth 0.5 points). In the end, this led to a total score of 13, with a maximum score of 6.5 for each Laterality (left, right).

Object Performance and Experience

The mean performance across all objects was 59% (S.D.=8.0%), with the maximum of 79%, and a minimum of 45%. The mean object experience (out of 9) was 6.30 (S.D.=1.86), with a maximum of 8.56, and a minimum of 3.67. The performance and experience for each object was recorded, with the means displayed in Table 1. The correlation between participants' mean experience and performance with each object was not significant, suggesting that for these objects, a participant's experience does not relate to their performance [$r(25) = .088, p = .471$]. (Table 1 about here).

Differences between left-hand and right-hand question scores are depicted using cumulative distribution functions, depicting the total probability of obtaining a specific score, and all scores less than it. The abscissa is the range of scores, and the ordinate is the total probability for a given score. Curves that are shifted to the right have less data points (participants) producing lower scores, and therefore their mean score would be higher than a curve that is shifted to the left.

Results

Novel Hand Imagery Questionnaire

Table 2 provides raw-score descriptive statistics to compare the movement imagery questionnaires and subscales. Participants' overall mean (SD) accuracy was .673 (.018). Using a 2 x 2 x 2 mixed ANOVA with the between-subjects factor of Perspective (FPV, uninstructed) and the within-subjects factors of Laterality (Right-Hand, Left-Hand) and Movement Type (Isolated Movement, Functionally-involved), a main effect of Laterality was found, demonstrating a hand-dominance effect with mean Right-Hand accuracy significantly greater than mean Left-Hand [$M_{\text{Right-Hand}} = .724 (.017), M_{\text{Left-Hand}} = .622 (.025); F(1,68) = 18.29, p < .001$,

$\eta_p^2 = .212$] . There was a main effect of Movement Type, with greater accuracy for Isolated-movement compared to Functionally-involved [$M_{\text{Isolated Movement}} = .757 (.019)$, $M_{\text{Functionally-involved}} = .588 (.021)$; $F(1,68) = 70.74$, $p < .001$, $\eta_p^2 = .510$]. The main effect of Perspective was not significant [$p > .1$]. A significant interaction between Laterality and Movement Type was observed, such that there was a stronger hand-dominance effect for functionally-involved imagined movements compared to Isolated Movements [$M_{\text{Functionally-involved Right-Left Difference}} = .141 (.026)$, $M_{\text{Isolated Hand Right-Left Difference}} = .062 (.023)$; $F(1,68) = 5.83$, $p < .05$, $\eta_p^2 = .079$] (Figure 2). (Figure 2 around here)

Relating the two subscales of isolated and functionally-involved movement imagery produced a relatively strong correlation, indicating that these two imagery processes do share some common source of variation [$r(68) = .52$, $p < .001$]. However, this correlation corresponds to only 27% of overall shared variance (i.e., r^2), indicating that these two processes still substantially differ from each other, which is evident from the interaction between Laterality and Movement Type, with functionally-involved imagery having a stronger hand-dominance effect. To ensure that the consistency in imagery ability between the two subscales is not entirely due to a shared relationship with any of the other questionnaires, we controlled for the four FPIQ subscales, as well as TAMIw, which produced a weaker, albeit significant correlation, eliminating the severity of a shared source of variability [$r_p(63) = .38$, $p < .01$]. (Table 2 around here).

FPIQ and TAMI

Scores for each of the FPIQ subscales were as follows: $M_{\text{kinesthetic}} = 8.67 (1.37)$, $M_{\text{position}} = 10.46 (1.82)$, $M_{\text{action}} = 10.61 (1.35)$, and $M_{\text{object}} = 10.40 (1.60)$. Though scores were near ceiling,

participants performed worse on the kinesthetic subscale compared to the other three (all p 's $< .001$). This pattern of results replicates the pattern of results reported in Madan and Singhal (2013) and the controls in Ochipa et al. (1997). The mean score on TAMlw was 16.90 (5.46).

Relationships between questionnaires

Hand Imagery Questionnaire and FPIQ

Both the FPIQ and our novel hand imagery questionnaire involved examining how people interact with objects. However, in our novel hand imagery questionnaire, only the functionally-involved movement subscale involved objects, whereas isolated movement questions did not. In looking at how our novel questionnaire relates to the FPIQ, we correlated each of our subscales to the four subscales of the FPIQ (Table 3). Measuring the degree to which these relationships could be the result of shared covariance was accomplished by running separate partial correlations. To differentiate isolated and functionally-involved movement imagery, partial correlations for the position and object subscales of the FPIQ were performed based on our prediction that functionally-involved movement imagery would strongly relate to these two FPIQ subscales. The partial correlation between isolated movement imagery and the position and object subscale was not significant [Isolated Movement-position: $r_p(66) = .043$ $p = .729$; Isolated Movement-object: $r_p(66) = .222$, $p = .069$]. When comparing isolated movement imagery to the object subscale of the FPIQ, the functionally-involved imagery questions were included as a control, since it also involved an understanding of various object parameters. (Table 3 about here).

Only the kinesthetic and object subscales of the FPIQ produced significant correlations with functionally-involved movement imagery (Table 3). Neither of the partial correlations

between functionally-involved imagery questions and the position or object subscales of the FPIQ were significant [Functionally-involved-position: $r_p(66) = .017, p = .890$; Functionally-involved-object: $r_p(66) = .212, p = .084$].

TAMlw, Hand Imagery Questionnaire, and Edinburgh Inventory Scale

TAMlw and its correlation with the entirety of the hand imagery questionnaire was ($r(68) = .490, p < .001$). The relationship between TAMlw and the two types of hand movement imagery is presented in Table 3. The relationship between the participants' Edinburgh Handedness score and their Laterality difference scores for both types of hand movement imagery depicted differences, notably that the isolated movement imagery subscale had a significant correlation with the EHI, whereas the functionally-involved imagery subscale did not [$r_{\text{Isolated-EHI}}(68) = .246, p < .05$; $r_{\text{Functionally-involved-EHI}}(68) = -.042, p > .05$].

Discussion

The present study sought to investigate two types of hand-related movement imagery. Functionally-involved movement imagery required participants to imagine hand-object interactions, whereas more abstract imagery processes required participants to imagine themselves making isolated hand-articulations. A significant laterality effect was observed for both isolated-movement and functionally-involved imagery, such that right-handed participants demonstrated greater performances for right-hand questions compared to left-hand questions. An interaction between Laterality and Movement Type further indicated that while both movement types involve hand-related movements, differences exist between isolated-movement and

functionally-involved movement imagery, with functionally-involved movements producing a greater hand-dominance effect.

In Sirigu and Duhamel's (2001) study with inferotemporal and left-parietal patients, they were unable to observe any immediate lateralization effects, and it is possible that this was due to the simplicity of the hand rotation task employed. There is supporting evidence to suggest imagined hand movements are in fact lateralized. Nico et al. (2004) demonstrated that amputee patients who underwent amputation of their preferred limb had higher latencies and made more errors on a left-right hand judgment task as compared to amputees of the non-dominant limb. Research employing hand laterality tasks have shown that right-handers recognize their dominant hand more easily compared to their non-dominant hand (Conson et al. 2011; Gentilucci et al. 1998; Ionta & Blanke 2009; Nì Choisdealbha et al. 2011). Further, it has been suggested that right-handers exhibit a heightened sense of ownership of their dominant hand (Hoover & Harris 2012, 2015). Moreover, when participants are required to imagine another person performing a motoric action, they imagine a significantly higher proportion of actions performed with their dominant rather than non-dominant hand, that is, right-handers report more right-handed actions compared to left-handers (Marzoli, Mitaritonna, et al. 2011; Marzoli, Palumbo et al. 2011; Marzoli, Menditto et al. 2013). Not all studies produce such simple findings however. Sabate et al. (2004) found lateralization in motor planning, but left-brain lesions affected the velocity of imagined movements in both hands, whereas right-brain lesions only affected left-hand imagined movements. Our results support their findings that suggest the left hemisphere dominates in planning complex sequences of movements in right-handed individuals. To further support the laterality effect that we observed, a mirrored version of the hand imagery questionnaire could be created, such that all left-hand questions become right-hand and vice-

versa. Doing so would eliminate the possibility that right-hand questions happened to be easier than left-hand questions.

The moderately strong correlation between our novel hand-imagery questionnaire and TAMI reflects the similarity between the two movement imagery questionnaires, but also demonstrates differences in the scale of body movement (hand vs. body) and degree of functional involvement (transitive vs. intransitive). This latter distinction is further demonstrated by the stronger relationship between TAMI and isolated movement imagery, compared to functionally-involved movement imagery. Both isolated hand and whole-body movement imagery are free of any transitive processes related to goal intention, which could reflect the unique variance in functionally-involved movement imagery ability. The observation that no significant partial correlations existed between either of the movement types and the FPIQ subscales suggests that the FPIQ subscales highly co-vary, making it difficult to further distinguish between isolated and functionally-involved movement imagery. Because the EHI is related to some degree with the mental simulations involving hands, we suggest that it may be thought of as a subjective movement imagery questionnaire itself. Subjective movement imagery questionnaires, such as the Vividness of Movement Imagery Questionnaire revised version (VMIQ-2; Roberts et al. 2008), require the participant to rate how vividly they can imagine themselves performing actions. Similarly, the EHI requires the participant to rate the degree to which they prefer using their right or left hand when performing certain actions. The relationship between the EHI and the isolated movement imagery Laterality score had a significant correlation as opposed to the relationship between the EHI and the functionally-involved movement imagery Laterality scores, which at first glance appears to be problematic. One would expect that imagined transitive movements oriented towards object interaction should be more

sensitive to hand dominance, and therefore produce a better indication of handedness. Marzoli et al. (2017) found that when required to imagine another person performing a manual action, right-handers imagining complex actions reported a larger proportion of right-handed actions compared with imagining simple actions, demonstrating a preference towards the dominant hand with increases in motor complexity. In fact, the functionally-involved movement imagery questions did produce a stronger handedness effect than the isolated movement imagery questions, suggesting that functionally-involved movement imagery utilizes additional factors predicting handedness.

There are several reasons why functionally-involved imagery does not closely relate to the EHI. The first regards the frame of reference evoked in both tasks. The EHI provides a single word for each object or action with no component evoking a particular reference frame, whereas the functionally-involved imagery subscale provides images of objects, which have been shown to induce egocentric spatial processing (Ruggiero et al. 2009). Promoting an egocentric frame of reference may allow more precise coordinate frames to be tapped into during imagery of hand movements, and could facilitate a stronger handedness effect. The functionally-involved imagery subscale may also differ from the EHI in terms of depth of processing. While the EHI simply requires participants to read a word and make a hand-preference judgment, the functionally-involved imagery subscale requires participants to not only imagine a series of finger movements to arrive at a final hand-shape, but to keep this final form in mind, and apply it to several objects in view. Functionally-involved movements may rely on more goal-oriented, lateralized motor imagery processes, and thus relate more strongly to handedness. Here, right-handed participants performed relatively poorer on the more memory demanding functionally-involved imagery subscale than on the isolated movement imagery subscale, which could also explain the

correlation observed between the isolated movement imagery subscale and the EHI. Depth of processing could also explain part of the distinction between the isolated and functionally-involved movement imagery subscales. The isolated movement subscale enables participants to match their imagined hand to an image of a hand that is visible, reducing the degree of working memory required. An interesting question going forward would involve modifying the isolated movement subscale to include questions where none of the images of hands were the correct final hand-shape, and thus the correct response would be “E” for “None”. Would participants be more likely to incorrectly pick one of the available options (using lower depth of processing) for non-dominant hand questions, and more likely to accurately select “None” (higher depth of processing) when imagining their dominant hand? Such a study would provide evidence to determine if a relationship exists between handedness and depth of processing.

Whether an individual is consciously aware of it or not, imagining a motoric action is done from either an egocentric (first-person) or allocentric (third-person) frame of reference. Movement imagery studies manipulating frame of reference can explicitly instruct the participant to use a particular perspective, or they can ask the participant after the experiment to report which imagery perspective they used. In the current study, we manipulated imagery perspective by either the presence or absence of an egocentric instruction. We manipulated frame of reference based on previous depictions of first-person instruction promoting an individual to primarily use motor resources, compared to third-person instructions which promote the use of visual resources when completing a mental rotation task (Sirigu & Duhamel 2001). Imagery perspective can interact with the lateralization of motor imagery on hand laterality tasks, such that an egocentric perspective speeds up the recognition of one’s own dominant hand (Conson et al. 2010, 2012; Ni Choisdealbh et al. 2011). The relative contribution of motor and visual

representation elicited as a function of imagery perspective has been depicted while individuals imagined others' actions (Marzoli, Mataritonna et al. 2011; Marzoli, Menditto et al. 2013). Specifically, a stronger activation of motor representation was elicited while a back-view/egocentric perspective was used, compared to a front-view/allocentric perspective (Marzoli, Palumbo et al. 2011). Further, perspective has been shown to influence the severity of such clinical disorders and post-traumatic stress disorder and social anxiety disorder, and can therefore pose as a new strategy for current therapeutic imagery interventions (Moran et al. 2015).

We did not observe any significant main effects when manipulating the frame of reference, however there are several explanations for this null result. The significance and strength of the effect may have been affected by the saliency of the manipulation. The egocentric instruction only appeared in the initial instruction package, and it is possible that increasing the salience by additional verbal instruction could have increased compliance. More likely, however, is the possibility that when given “uninstructed” instructions, individuals naturally imagine in an egocentric frame of reference, preventing a main effect from occurring. This is especially true if presenting images of objects or hands evokes an egocentric frame of reference. Lastly, it is possible that imagery perspective does not have an effect on imagery ability, however Roberts et al. (2008) demonstrated a higher correlation between external visual imagery (third-person) and the Movement Imagery Questionnaire (MIQ; Hall & Pongrac 1983; most recently the MIQ-RS [Movement Imagery Questionnaire - Revised, second version]; Gregg, Hall, & Butler 2010) compared to internal visual imagery (first-person). The MIQ-RS relies on incorporating information about form to accurately accomplish movements, and this information has been shown to be more readily acquired using external visual imagery (Callow & Hardy 2004). With

such evidence suggesting perspective influences imagery ability, future studies could require the participant to report which perspective they used at the end of the study. Such a method would still allow the main effect or any interactions to be observed, and the issue of compliance would be resolved.

Movement imagery, which is specific to imagining motoric actions, is just one type of imagery that belongs to the greater cognitive processes known as mental simulation, which encompasses all internally-driven sensorimotor activation. Mental simulation thus affords the ability to assess manipulability, or how readily an object can be manipulated. Rueschemeyer et al. (2010) distinguished two types of manipulability: functional manipulation for instances when the object can be used in a tool-like fashion, and volumetric manipulation involving those objects that cannot be used as a tool, but are still susceptible to interaction. The same group ran an fMRI study using a lexical decision task to investigate the differences between these two types of manipulability. By showing participants names of objects that fall under each manipulability type, they found differential neural activation of areas involved in movement imagery. Hand preference itself could be another construct of mental simulation, likely involving automatic processes of simpler sensory and motor networks to establish one's handedness. Our finding of an enhanced handedness effect for functionally-involved movement imagery, which incorporates more information such as the manipulability of objects, converges with the ideas surrounding embodied cognition, that our abstract cognitive processes arise from simpler and deeper processes such as our senses and ability to move.

Here we demonstrated that hand dominance influenced movement imagery ability for both isolated and functionally-involved hand movements. Our observation of a handedness effect in both isolated-movement and functionally-involved imagery processes is not surprising, due to

the common involvement of hand-related movements. The moderate correlation between the two movement types further indicates that although they share a common source of variability, these two types of movement imagery differ in some way. With the stronger handedness effect seen for functionally-involved movement imagery, it is possible that these two methods of measuring imagined hand movements differ in the degree of sensitivity to handedness. We propose that the functionally-involved imagery subscale differs from both the isolated movement subscale and the EHI in terms of requiring greater depth of processing, adding the construct of manipulability to the mental simulation of a hand movement by using object stimuli, and from the EHI alone by evoking an egocentric reference frame. It is possible that the EHI does not go far enough to elicit egocentric spatial processing, as the words presented in the EHI may in fact interfere with praxis. An objective hand imagery questionnaire that induces egocentric spatial processing and greater involvement of memory processes may act as a better skill-based measure of handedness.

References

- Alipour, A., Aerab-sheybani, K., & Akhondy, N. (2012). Effects of handedness and depth of processing on the explicit and implicit memory. *Procedia - Social And Behavioral Sciences*, 32, 29-33.
- Ankerst, M., Breunig, M., Kriegel, H., & Sander, J. (1999). OPTICS. *ACM SIGMOD Record*, 28(2), 49-60.
- Barsalou, L. (2008). Grounded Cognition. *Annual Review of Psychology*, 59(1), 617-645.
- Brodeur, M.B., Dionne-Dostie, E., Montreuil, T., & Lepage, M. (2010). The Bank of Standardized Stimuli (BOSS), a new set of 480 normative photos of objects to be used as visual stimuli in cognitive research. *PLoS ONE*, 5, e10773.
- Brodeur, M. B., Guérard, K., & Bouras M. (2014) Bank of Standardized Stimuli (BOSS) Phase II: 930 New Normative Photos. *PLoS ONE*, 9(9): e106953.
- Buccino, G., Binkofski, F., Fink, G., Fadiga, L., Fogassi, L., Gallese, V., et al. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *European Journal of Neuroscience*, 13(2), 400-404.
- Callow, N. & Hardy, L. (2004). The relationship between the use of kinaesthetic imagery and different visual imagery perspectives. *Journal Of Sports Sciences*, 22(2), 167-177.
- Chao, L. & Martin, A. (2000). Representation of manipulable man-made objects in the dorsal stream. *Neuroimage*, 12(4), 478-484.

- Conson, M., Aromino, A., & Trojano, L. (2010). Whose hand is this? Handedness and visual perspective modulate self/other discrimination. *Experimental Brain Research*, 206(4), 449-453.
- Conson, M., Mazzarella, E., & Trojano, L. (2011). Self-touch affects motor imagery: a study on posture interference effect. *Experimental Brain Research*, 215(2), 115-122.
- Conson, M., Mazzarella, E., Donnarumma, C., & Trojano, L. (2012). Judging hand laterality from my or your point of view: Interactions between motor imagery and visual perspective. *Neuroscience Letters*, 530(1), 35-40.
- Daszykowski, M., Walczak, B., & Massart, D. (2002). Looking for Natural Patterns in Analytical Data. 2. Tracing Local Density with OPTICS. *Journal of Chemical Information and Computer Sciences*, 42(3), 500-507.
- Epstein, M. (1980). The Relationship of Mental Imagery and Mental Rehearsal to Performance of a Motor Task. *Journal of Sport Psychology*, 2(3), 211-220.
- Flindall, J., & Gonzalez, C. (2013). On the evolution of handedness: Evidence for feeding biases. *PLoS ONE*, 8(11): e78967.
- Gentilucci, M., Daprati, E., & Gangitano, M. (1998). Right-handers and left-handers have different representations of their own hand. *Cognitive Brain Research*, 6(3), 185-192.

- Gerardin, E., Sirigu, A., Lehericy, S., Poline, J.B., Gaymard, B., Marsault, C., Agid, Y., & Le Bihan, D. (2000). Partially Overlapping Neural Networks for Real and Imagined Hand Movements. *Cerebral Cortex*, *10*(11), 1093-1104.
- 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.
- Guérard, K., Lagacé, S., & Brodeur, M. (2015). Four types of manipulability ratings and naming latencies for a set of 560 photographs of objects. *Behavior Research Methods*, *47*(2), 443-470.
- Hall, C., & Pongrac, J. (1983). Movement imagery questionnaire. London, Canada: University of Western Ontario.
- Hauk, O., Johnsrude, I., & Pulvermuller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron*, *41*, 301-307.
- Heath, M., Westwood, D., Roy, E., & Young, R. (2002). Manual asymmetries in tool-use: Implications for apraxia. *Laterality*, *7*(2), 131-143.
- Hoover, A., & Harris, L. (2012). Detecting delay in visual feedback of an action as a monitor of self-recognition. *Experimental Brain Research*, *222*(4), 389-397.
- Hoover, A., & Harris, L. (2015). The role of the viewpoint on body ownership. *Experimental Brain Research*, *233*(4), 1053-1060.

- Huth, A., de Heer, W., Griffiths, T., Theunissen, F., & Gallant, J. (2016). Natural speech reveals the semantic maps that tile human cerebral cortex. *Nature*, 532(7600), 453-458.
- Ionta, S., & Blanke, O. (2009). Differential influence of hands posture on mental rotation of hands and feet in left and right handers. *Experimental Brain Research*, 195(2), 207-217.
- Järveläinen, J., Schürmann, M., & Hari, R. (2004). Activation of the human primary motor cortex during observation of tool use. *Neuroimage*, 23(1), 187-192.
- Jeannerod, M. (1994). The representing brain: Neural correlates of motor intention and imagery. *Behavioral And Brain Sciences*, 17(02), 187.
- Just, M., Cherkassky, V., Aryal, S., & Mitchell, T. (2010). A neurosemantic theory of concrete noun representation based on the underlying brain codes. *PLoS ONE*, 5(1), e8622.
- Knecht, S., Dräger, B., Deppe, M., Bobe, L., Lohmann, H., Floel, A., Ringelstein, E., & Henningsen, H. (2000). Handedness and hemispheric language dominance in healthy humans. *Brain*, 123(12), 2512-2518.
- Madan, C.R., & Singhal, A. (2012). Motor imagery and higher-level cognition: Four hurdles before research can sprint forward. *Cognitive Processing*, 13(3), 211-229.
- Madan, C.R., & Singhal, A. (2013). Introducing TAMI: An objective test of ability in movement imagery. *Journal of Motor Behavior*, 45(2), 153-166.

- Madan, C.R., & Singhal, A. (2014). Improving the TAMI for use with athletes. *Journal of Sports Sciences*, 32(14), 1351-1356.
- Madan, C. & Singhal, A. (2015). No sex differences in the TAMI. *Cognitive Processing*, 16(2), 203-209.
- Madan, C., Chen, Y., & Singhal, A. (2016). ERPs differentially reflect automatic and deliberate processing of the functional manipulability of objects. *Frontiers In Human Neuroscience*, 10, 360.
- Marzoli, D., Mitaritonna, A., Moretto, F., Carluccio, P., & Tommasi, L. (2011). The handedness of imagined bodies in action and the role of perspective taking. *Brain And Cognition*, 75(1), 51-59.
- Marzoli, D., Palumbo, R., Di Domenico, A., Penolazzi, B., Garganese, P., & Tommasi, L. (2011). The Relation between Self-Reported Empathy and Motor Identification with Imagined Agents. *PLoS ONE*, 6(1), e14595.
- Marzoli, D., Menditto, S., Lucafò, C., & Tommasi, L. (2013). Imagining others' handedness: visual and motor processes in the attribution of the dominant hand to an imagined agent. *Experimental Brain Research*, 229(1), 37-46.
- Marzoli, D., Lucafò, C., Rescigno, C., Mussini, E., Padulo, C., & Prete, G. et al. (2017). Sex-specific effects of posture on the attribution of handedness to an imagined agent. *Experimental Brain Research*, 235(4), 1163-1171.
- Mills, K., Gibb, R., MacLean, J., Netelenbos, N., & Gonzalez, C. (2015). The relationship between motor lateralization and executive function. *International Journal Of Developmental Neuroscience*, 47, 89.

- Moran, A., Bramham, J., Collet, C., Guillot, A., & MacIntyre, T. (2015). Motor imagery in clinical disorders: importance and implications. *Frontiers in Psychiatry, 6*, 1-4.
- Ní Choisdealbha, Á., Brady, N., & Maguinness, C. (2011). Differing roles for the dominant and non-dominant hands in the hand laterality task. *Experimental Brain Research, 211*(1), 73-85.
- Nico, D., Daprati, E., Rigal, F., Parsons, L., & Sirigu, A. (2004). Left and right hand recognition in upper limb amputees. *Brain, 127*(1), 120-132.
- Ochipa, C., Rapcsak, S., Maher, L., Rothi, L., Bowers, D., & Heilman, K. (1997). Selective deficit of praxis imagery in ideomotor apraxia. *Neurology, 47*, 474-480.
- Oldfield, R. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia, 9*(1), 97-113.
- Porro, C., Francescato, M., Cettolo, V., Baraldi, P., & Diamond, M. (1996). Primary motor cortex activity during motor performance and motor imagery: A fMRI study. *Neuroimage, 3*(3), S214.
- Pujol, J., Deus, J., Losilla, J.M., & Capdevila, A. (1999). Cerebral lateralization of language in normal left-handed people studied by functional MRI. *Neurology, 52*, 1038-43.
- Roberts, R., Callow, N., Hardy, L., Markland, D., & Bringer, J. (2008). Movement imagery ability: Development and assessment of a revised version of the Vividness of Movement Imagery Questionnaire. *Journal of Sport & Exercise Psychology, 30*, 200-221.

- Roth, M., Decety, J., Raybaudi, M., Massarelli, R., Delon-Martin, C., & Segebarth, C. (1996). Possible involvement of primary motor cortex in mentally simulated movement. *Neuroreport*, 7(7), 1280-1284.
- Rueschemeyer, S., van Rooij, D., Lindemann, O., Willems, R., & Bekkering, H. (2010). The function of words: Distinct neural correlates for words denoting differently manipulable objects. *Journal Of Cognitive Neuroscience*, 22(8), 1844-1851.
- Ruggiero, G., Ruotolo, F., & Iachini, T. (2009). The role of vision in egocentric and allocentric spatial frames of reference. *Cognitive Processing*, 10(S2), 283-285.
- Ruthsatz, V., Neuburger, S., Jansen, P., & Quaiser-Pohl, C. (2015). Cars or dolls? Influence of the stereotyped nature of the items on children's mental-rotation performance. *Learning and Individual Differences*, 43, 75-82.
- Sabaté, M., González, B., & Rodríguez, M. (2004). Brain lateralization of motor imagery: motor planning asymmetry as a cause of movement lateralization. *Neuropsychologia*, 42(8), 1041-1049.
- Saccuman, M., Cappa, S., Bates, E., Arevalo, A., Della Rosa, P., Danna, M., & Perani, D. (2006). The impact of semantic reference on word class: An fMRI study of action and object naming. *Neuroimage*, 32(4), 1865-1878.
- Sirigu, A., and Duhamel, J. (2001). Motor and visual imagery as two complementary but neurally dissociable mental processes. *Journal of Cognitive Neuroscience*, 13(7), 910-919.

Willems, R. M., Labruna, L., D'Esposito, M., Ivry, R., & Casasanto, D. (2011). A functional role for the motor system in language understanding: Evidence from Theta-Burst Transcranial Magnetic Stimulation. *Psychological Science*, 22, 849 -854.

Yang, J., and Shu, H. (2013). Passive reading and motor imagery about hand actions and tool-use actions: an fMRI study. *Experimental Brain Research*, 232(2), 453-467.

Table 1. Mean object experience and performance for each of the objects. Mean accuracy score determined as unique proportion of obtained versus total points accumulated from each question involving the object. Objects are listed based on their names in the BOSS (Brodeur et al. 2014) database.

Objects	Average Experience (0-9)	Average Score (0-1)
calculator(01)	8.3	0.56
bagel(01)	6.8	0.79
rearviewmirror	5.3	0.67
binoculars(01b)	4.3	0.59
dropper(01)	6.0	0.68
scissors(01)	8.2	0.57
pencil(01)	9.0	0.64
computer mouse(06)	8.4	0.61
mousetrap	2.3	0.65
dice(05a)	6.5	0.71
carkey	6.4	0.63
cigarette	1.9	0.53
gamepiece	5.8	0.58
spraybottle(01)	6.7	0.66
weight(01)	6.3	0.58
soapdispenser(01)	7.9	0.51
plate(01b)	8.7	0.57
hammer(01)	5.7	0.51
iron(01b)	4.9	0.52
eraser	8.4	0.58
envelope(03a)	7.0	0.64
deodorant(02a)	7.1	0.65
nailclipper(03b)	8.0	0.45
thumbtack(02a)	6.3	0.45
lunchbox	5.8	0.51
punchingbag	4.2	0.51
syringe(01)	4.0	0.51

Table 2. Descriptive statistics of raw scores for all movement imagery measures and subscales.

	<i>M</i>	<i>SD</i>	Possible range	Observed range
Isolated Movement	8.329	1.886	0 – 11	2 – 11
Functionally-involved	3.825	1.415	0 – 6.5	0 – 6.5
FPIQ-Kinesthetic	8.671	1.372	0 – 12	4 – 12
FPIQ-Position	10.457	1.815	0 – 12	5 – 12
FPIQ-Action	10.614	1.354	0 – 12	4 – 12
FPIQ-Object	10.400	1.598	0 – 12	6 – 12
TAMIw	16.857	5.462	0 – 24	4 – 24

Table 3. Correlations (*r*) between the Isolated Movement (IM) and Functionally-involved Movement (FM) subscales with the FPIQ, TAMIw, and EHI.

* = $p < .05$; ** = $p \leq .001$.

	Isolated (IM) <i>r</i>-coefficients	Functionally-Involved (FM) <i>r</i>-coefficients
FPIQ-Kinesthetic	.257*	.337*
FPIQ-Position	.255*	.194
FPIQ-Action	.335*	.211
FPIQ-Object	.436**	.353*
TAMIw	.529**	.288*
EHI (hand-diff. score)	.246*	-.042

Figure 1: Example of Isolated Movement (A) and Functionally-Involved (B) question types.






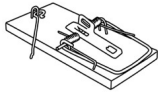


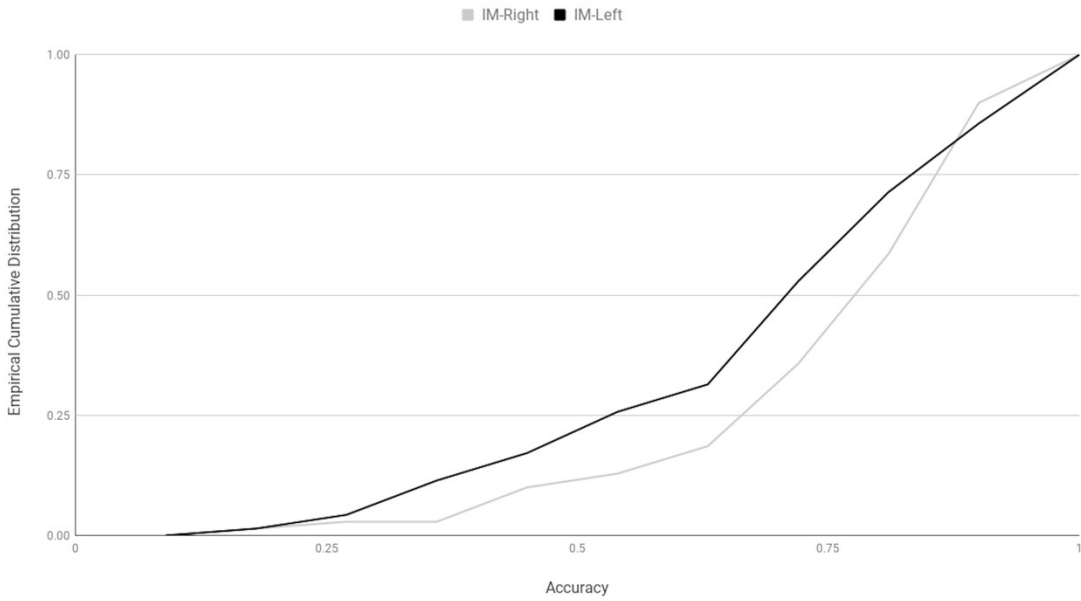
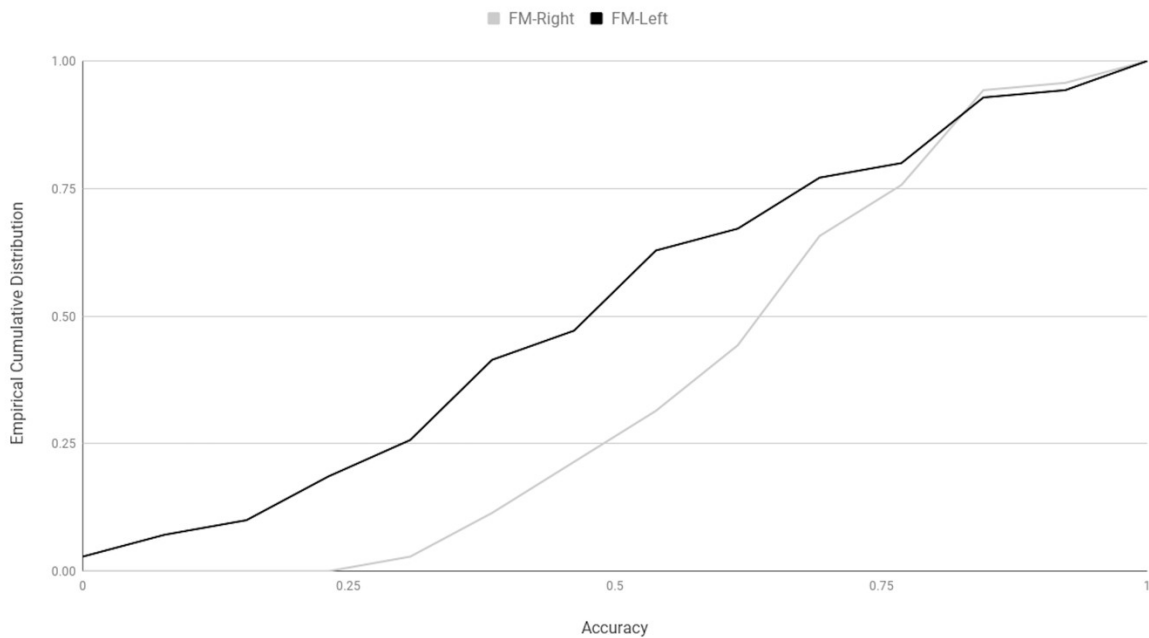
<p>A Which of the following is most similar to your imagined hand form?</p> <p>A) </p> <p>B) </p> <p>C) </p> <p>D) </p> <p>E) Unclear</p>	<p>B Which of the following objects would you most likely use with the imagined hand form?</p> <p>A)  Game Piece</p> <p>B)  Mouse Trap</p> <p>C)  Car Key</p> <p>D)  Calculator</p> <p>E) Unclear</p>
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Figure 2: Proportion of participants' accuracy on Isolated Movement (IM)-Right versus IM-Left subscales (A). Proportion of participants' accuracy on Functionally-involved Movement (FM)-Right versus FM-Left subscales (B).

A) Isolated hand movement sub-scale



B) Functionally-involved movement sub-scale



In Chapter 2, we set out to create a hand-version of the Test of Ability in Movement Imagery (TAMI) to create an objective mental imagery questionnaire that could induce hand-dominance effects. In theory, the observation of a hand-dominance effect, such that subjects perform better on items involving imagined movements of their dominant versus non-dominant hand, would suggest the mental simulation is lateralized, activating the motor cortex in the cerebral hemisphere contralateral to the right or left hand.

Behaviorally, we demonstrated a right-hand dominance effect in right-handed participants while they performed a pencil-and-paper hand-version of the TAMI. Specifically, right-handed participants scored higher on right-hand items compared to left-hand items. This effect was statistically significant for the Isolated-movement trials, and even more statistically significant for Functionally-involved trials (see Chapter 2 for descriptions of these types of trials). An interaction effect was observed, such that right-hand dominance effect was greater for Functionally-involved trials compared to Isolated movement trials. Given the extant literature depicting event-related desynchronization in the mu frequency-band (8-13 Hz) over the primary motor cortex at the onset of both overt and imagined movements, we set out to measure the electrophysiology that drove our handedness effect. Chapter 3 describes this EEG study, that included both right- and left-handed participants, in attempt to additionally obtain a left-hand dominance effect, as well as detect lateralized mu suppression in both participant-handedness groups. Previously, Lambert and others (in-press) carried out an EEG study using the original TAMI, which involved imagining whole-body movement instructions followed by selecting a final body position that matched the one they constructed in their mind. Chapter 3 describes our intent to replicate and extend the findings from this whole-body TAMI EEG study, which found enhanced mu suppression for correct versus error trials. This work aligns with developing valid

and reliable objective measures of mental imagery, which are useful feedback tools to assist brain-computer interfaces, as well as training tools in neurorehabilitation clinics.

The work described in Chapter 3 closely followed the paradigm used in the whole-body TAMI EEG study, with both differing from the behavioral pencil-and-paper versions by introducing fixed intervals between movement instructions. The hand-version of TAMI only used Isolated-movement trials from the study in Chapter 2, in an attempt limit the manipulation between the whole-body and hand-version TAMI to these anatomical changes. However, the finger movement instructions did not precisely replicate those in the whole-body version, as they had to be tailored to describe possible finger movements. Additionally, to prevent ceiling effects, some finger movement instructions involved several fingers moving in the same manner within one instruction, whereas the whole-body TAMI had one body-part moving per instruction. Chapter 3 reports the findings from this hand-version TAMI EEG study, and given the pattern of results obtained, discusses important qualities of both imagery questionnaires that may have driven the observed effects.

Chapter 3:

Objective Test of Imagined Hand-Manipulations Elicits Spatial Imagery

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Abstract

Previous studies on hand-related movement imagery have observed event-related desynchronization (ERD) over C3 and C4 electrodes, measuring the activity prior to explicit movement onset. The majority of these studies employ tasks that require gross hand rotations, reaching, and grasping actions, involving single, goal-oriented movements. The present study sought to utilize the novel objective Test of Ability in Movement Imagery (TAMI) developed by Madan and Singhal (2013), focusing on hand movements while EEG data was recorded. Both right- and left-handed participants completed this objective, multiple-choice style, in addition to a battery of extant movement imagery questionnaires. An interaction was observed, such that greater proportions of frontal-midline theta oscillations and posterior parietal alpha were detected during successful versus unsuccessful trials. No behavioral hand-dominance effect was replicated, nor were any lateralized ERD detected as a function of participant or item handedness. We propose that the computerized version of the hand-imagery task presented here differed from earlier hand and whole-body versions with respect to cognitive load, forcing participants to use spatial working memory to successfully perform the task. Future studies will require specific manipulations in an attempt to tease apart motor versus spatial imagery processes.

Keywords: spatial imagery; objective test; working memory; visualization

Drs. Anthony Singhal, Chris R. Madan, Mr. Jonah Elke, and Mr. Christopher M. Donoff have no conflicts of interest or financial ties to disclose.

Introduction

Imagine you are running to catch a bus that has started to depart without you. You feel your heart pounding, and perhaps you can't run your fastest because of a heavy backpack that keeps thudding against your lower back. People vary in how vividly they can mentally simulate the different sensori-motor modalities one experiences. Mental simulation, also referred to as mental imagery, refers to this top-down process in which our sensory experiences set the degrees of freedom for simulations of both past experiences (episodic memory) and constructed novel experiences. Commonly studied types of mental imagery include visual (Palmiero et al., 2009; Dijkstra et al., 2019), auditory (Martin et al., 2018; Pruitt, Halpern, & Pfordresher, 2019), olfactory (Del Gratta et al., 2001), spatial (Farah et al., 1988; Kozhevnikov, Kosslyn, & Shepard, 2005) and motor (Callow & Hardy, 2004; Heremans et al., 2011; Wilson et al., 2016; Filgueiras, Quintas Conde, & Hall, 2018; Lebon et al., 2018). Motor imagery is further broken down into kinesthetic motor imagery (KMI), which requires simulating the sensation of movement from a egocentric frame of reference, and visual motor imagery (VMI), which requires self-visualization of a movement in egocentric or allocentric frames of reference (Toriyama, Ushiba, & Ushiyama, 2018). It is important to note that the motor imagery literature does not always explicitly state which subtype is being investigated, with the term 'motor imagery' often defaulting to refer to KMI. As identified by Madan and Singhal (2012), it is paramount that researchers develop a clear and consistent nomenclature when identifying the type of mental imagery believed to be elicited and measured.

Of importance to the present study, there is a distinction between motor imagery and spatial imagery. Motor imagery necessitates an internal representation of a given motor act accompanied by subliminal activation of the motor system in the absence of overt motor output

(Jeannerod, 1994; Sabaté, González, & Rodríguez, 2004). Further, it has been suggested that imagining motoric movements through an egocentric frame of reference enhances the vividness of motor imagery compared to allocentric frames of reference by increasing the simulation of kinesthetic sensation (Sirigu & Duhamel, 2001). The electroencephalography (EEG) motor imagery literature has observed a similar event-related desynchronization (ERD) over the sensorimotor cortex that arises at the onset of explicit motoric movements (Pfurtscheller et al., 2006; Nam et al., 2011). This desynchronization occurs in the mu frequency band (8-13 Hz), and is also commonly referred to as mu-suppression. This has led researchers to propose motor imagery reactivates secondary motor cortex regions, such as the supplementary motor area (SMA) and medial premotor cortex (mPMC), which has been supported by my fMRI studies (Héту et al., 2013; Taube et al., 2015). Distinctions between left- and right-hand dominant participants have been demonstrated, such that right-hand dominant participants produce greater activity in the inferior/middle temporal cortex, pre-central sulcus, and post-central sulcus of the left hemisphere compared to the right hemisphere (Willems et al., 2009). Left-handers show a weaker reversal of this pattern, with significant increases in right-hemisphere post-central sulcus compared to the left hemisphere. Further, support that common neural correlates are activated during explicit and imagined movements comes from literature depicting embodied experience effects on motor imagery ability (Conson, Mazzarella, & Trojano, 2011; Guillot, Moschberger, & Collet, 2013). Priming effects occur, such that explicitly performing the physical movements before imagining them improves the imagery ability of the participants (Williams, Cumming, & Edwards, 2011). Spatial imagery involves internally directed attention towards the evaluation and manipulation of spatial features (Kozhevnikov, Kosslyn, & Shepard, 2005). These kinds of simulations activate regions along the dorsal pathway of the visual system, providing processes

for planned action, object localization, and proprioception (Fiehler & Roesker, 2010; Pilacinski, Wallsheid, & Lindner, 2018). Possessing the ability to understand spatial properties of objects and the environment is an important component of motor-planning and decision making. The dorsal fronto-parietal network (dFPN) is involved in a variety of functions including motor-planning, spatial attention, and working memory (Ptak, Schnider, & Fellrath, 2017). The dFPN's versatility has led some to posit that over time it has shifted from a pure motor-control network to a domain-general system that provides a space to emulate dynamic representations of abstract actions and spatial features (Fellrath et al., 2016). The degree to which the dFPN is elicited during motor imagery tasks will likely depend on properties that influence working memory and spatial cognition, such as cognitive load and complexity of action. Further, actions can be designated as either being transitive (using objects/tools to achieve a particular goal) or intransitive (without using any objects or tools to accomplish a goal; see Chapter 1). Tasks that vary in the type of action required (transitive versus intransitive) have been shown to differentially activate the dFPN (Schulz et al., 2018; see Chapter 1). Developing tasks that limit participants to engage in a particular type of imagery (e.g., motor, spatial, visual, etc.) are growing in demand, as the success of brain-computer interfaces and neurorehabilitation programs require tasks that provoke neural activity in consistent and specific regions of the brain. Trying to induce reliable and valid forms of imagery leads to the distinction between two general types of mental imagery measures.

When investigating mental imagery, experimenters can either rely on subjective self-reports of imagery vividness, or use objective tests that provide insights to imagery ability based on task performance. There are costs and benefits to using either approach, making selection dependent on the research question. Subjective assessments risk introducing the confounding

variables of inflated confidence or social desirability bias, especially with specific populations such as athletes (McKelvie, 1995). Subjective questionnaires prompt more holistic features of imagined contents to be attended to, such as the form, size, shape, color, or brightness of an object or scene (McAvinue & Robertson, 2007). Objective measures induce more specific representations of the spatial relations between objects, the location and movement of objects in space, and other complex spatial transformations, but are therefore limited in scope (Blajenkova, Kozhevnikov, & Motes, 2006). Indexes of imagery accuracy obtained from objective tasks are not a measure of imagery vividness directly. It is assumed that the accuracy a participant exhibits on a given task indicates their ability to control and form mental images effectively. Participant compliance is particularly difficult to control when studying mental imagery, as their successful behavior does not necessitate the utility of specific mental imagery processes. Objective tests in combination with neuroimaging do enable the experimenter to eventually determine which cognitive processes were used for a given task. Obtaining accuracy scores from tasks that are shown through neuroimaging to necessitate the recruitment of mental imagery is useful in several ways. One, this measure can be compared between particular populations (e.g., mathematicians vs. control) to uncover which behaviors are influenced by imagery ability. Second, the ability to code individual imagery events as ‘accurate’ versus ‘inaccurate’ is useful for brain-computer interfaces that are learning to decode EEG data based on performance. The work presented here utilized a hand-version of the objective Test of Ability in Movement Imagery (TAMI; Madan & Singhal, 2013, 2014). The TAMI is an objective measure of whole-body movement imagery, in which participants imagine a sequence of five limb and torso movements, and match their final imagined body position to one of five hand-drawn images. In this way, participants can objectively get each item correct or incorrect depending on the

accuracy of their mental image. A recent EEG study observed mu-suppression (ERD) over electrode sites C3 and C4 for correct trials versus incorrect trials on this task (Lambert et al., In-press). This observation suggests the successful performance of movement imagery involves motor planning processes, in which ERD over central sites is an index of. Here, TAMI was adapted to involve hand-movements, to specifically induce the imagination of these fine-motor movements, obtain an index of this ability, and relate this index to the level of mu-suppression observed, as well as other measures of mental imagery. Specifically, the present study included the original TAMI, a hand-preference screening tool (Edinburgh Handedness Inventory; Oldfield, 1971), the Mental Rotation Task (Peters, 1995), and the Florida Praxis Imagery Questionnaire (Ochipa et al. 1997). The TAMI is being included to help determine how the ability to image fine-motor movements of the hand relates to imagined whole-body movements. The inclusion of this objective test will also serve as a means of providing some convergent validity, as the present study is replicating the paradigm of TAMI, but manipulating the instructions to involve hand-related movements. The inclusion of the Edinburgh Handedness Inventory will provide an index of hand preference that places a participant on a spectrum of hand preference, from ambidextrous to strong right- or left-hand preference. Such an index can be related to accuracy scores, as well as lateralized oscillatory activity. To better understand the imagery processes involved in completing the hand-version of TAMI, the Mental Rotation Task and Florida Praxis Imagery Questionnaire have been included, the former a measure of one's ability to form and manipulate visuospatial mental representations, and the latter a measure of the ability to simulate properties such as direction or spatial location of objects in the mental representations of tools/non-tools and limb/hand movements. The degree to which the novel

hand-imagery task here relates to these two measures of mental imagery will inform on the type of information being represented to successfully complete the task.

The present study sought to extend the results from Lambert et al. (In-press) and Donoff et al. (2018), using a hand-version of the objective Test of Ability in Movement Imagery (TAMI; Madan & Singhal, 2013, 2014). Event-related desynchronization (mu suppression) has been observed for correct trials of TAMI, indicating motoric simulation was used to perform the task (Lambert et al., In-press). Further, a hand-dominance effect was observed using the hand-version of TAMI (Donoff et al., 2018), with right-handed participants performing better for right-hand versus left-hand items. These results led the present authors to predict an interaction between a participants' handedness, the laterality of the item (left or right hand), oscillatory activity detected, and accuracy. Specifically, right-handed participants should depict more mu suppression for accurate trials involving the simulated action of their dominant (right) hand, and left-handed participants should depict more mu suppression for accurate trials involving their dominant (left) hand. Observing such a result would confirm that the hand-version of the TAMI evokes motor imagery processes to successfully complete the task, as well as support the extant literature depicting mu suppression at the onset and duration of motor simulation.

Methods

Participants

A total of 40 undergraduate students (18 left-handed; 29 female) the average age of 19.23 ($SD = 1.42$) participated to earn credit towards an introductory undergraduate psychology course. Students' handedness was measured using the Edinburgh Handedness Inventory, where a Laterality Quotient (LQ) of 50 indicates ambidexterity [$M_{\text{right-handed}}$ (SD) LQ = 87.33 (11.40); $M_{\text{left-}}$

handed (SD) LQ = 11.29 (14.53)] (Oldfield, 1971). Data from 14 participants were excluded from analysis: 11 were excluded due to excessive amounts of artifacts detected in the EEG due to a broken net, and three due to an ambidextrous score of 50 on the EHI. All participants had normal or corrected-to-normal vision. Written consent was obtained and the research protocol was approved with the consent of the University of Alberta research ethics board.

Materials

Hand-Imagery Questionnaire

The hand-imagery questionnaire employed in Donoff et al. (2018) is an adaptation of the TAMI developed by Madan and Singhal (2013, 2014). Where TAMI investigated mental imagery of whole-body movements, the adaptation focused on hand-movements. In Donoff et al. (2018), participants were presented with Isolated-movement (intransitive) and Functionally-involved (transitive) trials. Here, only Isolated-movement trials were presented in an attempt to replicate the paradigm used by Lambert et al. (in-press). The computer program of the task was created using E-Prime 2.0 presentation software (Psychology Software Tools, Pittsburgh, PA). Each question began with an image of an open hand, to depict the initial starting position. Five hand-movement commands followed, in which the participant was required to read and mentally perform the series of hand movements until arriving at a final hand position. An example of the five finger-movement instructions is as follows: “1. Lay your hand open, palm up, with your fingers together. 2. Spread your fingers apart. 3. Cross your pinky finger in front of your ring finger. 4. Point your middle finger perpendicular to the palm. 5. Touch the tip of your thumb midway up your middle finger.” Each hand-movement command appeared sequentially, and remained on the screen until all five commands had been presented. A command would be

displayed for 5000 ms until the next command appeared automatically. After the fifth command, a response screen appeared, prompting the participant to input a response ‘A’ through ‘D’ corresponding to the final hand position they imagined. Participants could also respond ‘E’ for ‘Unclear’. Participants held a tennis ball in the hand they were creating a mental image of, to provide a natural, uniform hand position across participants, also reducing the frequency of explicit hand movements. The computerized version contained 20 trials consisting of two blocks: Right-hand and Left-hand. It was randomized which block would come first. For descriptions of how the hand stimuli and commands were derived, please refer to Donoff et al. (2018).

Test of Ability in Movement Imagery (TAMI) and Florida Praxis Imagery Questionnaire (FPIQ)

In the present study, the same computerized version of TAMI was employed as it appears in Lambert et al. (in-press). The TAMI is a multiple-choice style questionnaire that assesses an individual’s ability to imagine whole-body movements. For each question, participants first read and imagine themselves perform a series of five consecutive limb- or torso-movements. Five images of final body positions are then displayed, in which the participant selects the body position that matches their mental image. Consisting of 10 items, we used an alternate scoring method (TAMIw) to reduce ceiling effects by assigning more weight to the more difficult questions, making the test out of 24 points (Madan & Singhal, 2014).

The FPIQ assesses mental imagery ability by providing ‘A or B’ questions on qualities of motoric movements and objects. The questionnaire is comprised of four subscales: Position, Kinesthetic, Object, and Action. Both the TAMI and FPIQ are objective tests of mental imagery, measuring task accuracy that purportedly requires mental imagery, as opposed to obtaining

subjective indexes of imagery vividness. For more detailed descriptions of both the TAMI and FPIQ used in the present study, please refer to Donoff et al. (2018).

Mental Rotation Task (MRT)

The MRT is an objective test of visual imagery originally developed by Shepard and Metzler (1971). This task presented two abstract three-dimensional block-object images, requiring the participant to mentally rotate one to determine if it is the same as the other. In the present study, we used MRT-A by Peters (1995), a redrawn version of the Vandenberg and Kuse (1978) MRT, which provides a target block-object image, followed by four samples. Participants are required to select the two sample images that are identical to the target image, by mentally rotating each image. No partial grades were awarded for selecting only one sample image correctly. There are two types of trials: original block figures from Shepard and Metzler (1971), as well as three-dimensional figurines of bodies in different conformations. This pencil-and-paper questionnaire is comprised of 24 items (12 of which are figurines).

Edinburgh Handedness Inventory (EHI)

The EHI was developed by Oldfield (1971) and is a 10-item questionnaire designed to measure handedness. Here we created a computerized version of the EHI, in which participants first indicated hand preference by pressing ‘1’ for left hand, ‘2’ for right hand, or ‘3’ for neither (ambidextrous). If either the left or right hand was chosen, they were further prompted to indicate the strength of this preference, with ‘1’ indicating moderate (infrequently using the non-dominant hand for the given task/object), and ‘2’ indicating strong (never using the non-dominant hand for the given task/object). The Laterality Quotient (LQ) here was calculated as an

index of right handedness, where 100 is completely right handed, and 50 indicates no preference (ambidextrous). The 10 items were: writing, drawing, throwing, scissors, toothbrush, knife (without fork), spoon, broom, striking a match (match), and opening a box (lid).

Procedure

All participants completed the questionnaires in the following fixed order: hand-imagery questionnaire, TAMI, EHI, MRT, and FPIQ.

Prior to beginning the hand-imagery questionnaire, participants were provided verbal, as well as written instruction describing the types of questions they would be answering.

Specifically, extra emphasis was provided to remind participants to hold the tennis ball in the same hand that appeared at the beginning of each trial. Examples of either pointing your thumb “*parallel*” or “*perpendicular to the plane of your palm*” were provided to reduce potential confounds due to participants misunderstanding the instructions. Participants completed the hand-imagery questionnaire, TAMI, and EHI on the computer, followed by pencil-and-paper versions of the MRT and FPIQ outside of the chamber.

Data Analyses

EEG Recording

EEG was recorded using a 256-channel high-density array net (Electrical Geodesics Inc., Eugene, OR). The signal was amplified using a Net Amps 300 amplifier and sampled at 250 Hz, with impedance being kept below 50k Ω . Recording was initially referenced to the vertex electrode (Cz), and was later average re-referenced. Preprocessing and time-frequency analyses were performed using custom MATLAB scripts, in conjunction with open source toolboxes

(EEGLAB; Delorme and Makeig, 2004) and the Better OSCillation Detection Method (BOSC; Whitten et al., 2010). Artifact rejection was performed using independent component analysis in EEGLAB, with the selection of components based on visual inspection of the spatial topographies and power spectral characteristics. A 36 ms time-lag correction was performed to adjust event latencies due to a known hardware calibration problem identified by EGI.

After preprocessing, the epoched EEG data was analyzed for oscillations using the BOSC method (see Chapter 1), which utilizes both a power and duration threshold, providing a conservative approach to detecting rhythmic activity (Caplan et al., 2001; Whitten et al., 2010). Segments of signal were classified as oscillatory when the power at a given frequency exceeds the power threshold for a minimum duration of time. A duration threshold of three cycles was selected to ensure that abrupt increases in power were not considered oscillatory. The result is the P_{episode} measure, which represents the proportion of oscillations detected by BOSC at a given frequency during a given epoch.

Five electrode sites (Cz, C3, C4, Fz, and Pz) were selected for analysis based on apriori predictions of motor involvement. Specifically, we expected C3 and C4 sites to contain mu oscillations (8-13 Hz), as previously observed (Formaggio et al., 2010; Pfurtscheller & Neuper, 1997; Pfurtscheller et al., 2006; Pfurtscheller et al., 2005; Nam et al., 2011; McFarland et al., 2000). By also selecting Fz and Pz sites, detection of the recruitment of processes beyond movement imagery could be made. Similar tasks involving sequential memory have depicted posterior alpha (8-13 Hz) and frontal-midline theta (3-7 Hz) oscillations, thought to represent the utility of spatial working memory processes (Sack et al., 2008; Berryhill & Olson, 2008). Frequencies within the alpha- and theta-bands were collapsed by averaging together the P_{episode}

values. Analysis was focused on comparing the proportion of oscillations detected in each frequency band across electrode sites as a function of correct and incorrect trials.

Statistical analyses

A five-way mixed ANOVA was conducted using a linear mixed-effects model with the nlme and ezANOVA R packages (Lindstrom & Bates, 1988; Bakeman, 2005). Using the linear mixed-effects model allows for within-subject errors to covary and/or have unequal variances. The between-subject factor was Hand-dominance (Right, Left), and the within-subject factors were Item-laterality (Right-image, Left-image), Site (C3, C4, Cz, Pz, and Fz), Frequency (Alpha, Theta), and Accuracy (Correct, Incorrect). Correlations were also calculated between the performance on the hand-imagery questionnaire and the other questionnaires (TAMI, MRT, EHI and FPIQ).

Results

Behavioral Results

An overall view of performance on the mental imagery questionnaires was obtained. Table 1 provides raw-score descriptive statistics to compare all the mental imagery questionnaires and subscales. Participants' overall mean (SD) accuracy on the hand-imagery questionnaire was .738 (.206). Scores for each of the FPIQ subscales were as follows: $M_{\text{kinesthetic}} = 8.97 (1.44)$, $M_{\text{position}} = 10.65 (1.92)$, $M_{\text{action}} = 10.21 (1.55)$, and $M_{\text{object}} = 10.51 (1.35)$. This pattern of results replicate the pattern of results reported in Donoff et al. (2018) and Madan and Singhal (2013). The mean score on TAMIw was 16.93 (3.22). There was no significant Hand-dominance effect observed when comparing Item-laterality performance in both right- and left-handed

participants [$M_{\text{Right Right-image}} = .679 (.237)$, $M_{\text{Right Left-image}} = .689 (.212)$, $M_{\text{Left Right-image}} = .647 (.391)$, $M_{\text{Left Left-image}} = .642 (.231)$; $F(1,22) = 1.251$, $p > .05$, $\eta_p^2 = .116$]. (Table 1 here).

Oscillations

Running the linear mixed-effects model and ANOVA on the between-subject factor of Hand-dominance (Right, Left) and the within-subject factors of Item-laterality (Right-hand, Left-Hand), Site (C3, C4, Cz, Pz, and Fz), Frequency (Alpha, Theta), and Accuracy (Correct, Incorrect), a two-way interaction was observed between Frequency and Site. The proportion of alpha oscillations detected was greater at Pz compared to Cz, whereas the proportion of theta oscillations detected was greater at Fz compared to Cz [$M_{\text{alphaPepisode Pz}} = .152 (.019)$, $M_{\text{alphaPepisode Cz}} = .118 (.021)$, $M_{\text{thetaPepisode Fz}} = .147 (.039)$, $M_{\text{thetaPepisode Cz}} = .092 (.031)$; $F(4,16) = 4.801$, $p < .001$, $\eta_p^2 = .210$]. This higher-order interaction is explained by a two-way interaction observed between Accuracy and Frequency. Here, a greater proportion of alpha oscillations was detected at Pz for Correct versus Incorrect trials, and a greater proportion of theta oscillations detected at Fz and Pz for Correct versus Incorrect trials [$M_{\text{alphaPepisode Pz Correct}} = .161 (.041)$, $M_{\text{alphaPepisode Pz Incorrect}} = .129 (.121)$, $M_{\text{thetaPepisode Fz Correct}} = .159 (.039)$, $M_{\text{thetaPepisode Fz Incorrect}} = .125 (.067)$, $M_{\text{thetaPepisode Pz Correct}} = .164 (.022)$, $M_{\text{thetaPepisode Pz Incorrect}} = .122 (.043)$; $F(4,6) = 3.462$, $p < .001$, $\eta_p^2 = .487$]. P_{episode} as a function of frequency for Correct versus Incorrect trials at Pz and Fz is depicted in Figure 1. Mu was detected during this task, but did not differ as a function of accuracy [$p > .1$].

Topographic maps were generated to capture the full distribution of activity in the theta (3-7 Hz) and alpha (8-13 Hz) band ranges. Figure 2 depicts the increased alpha activity over parietal regions during Correct trials, and increased theta activity over frontal regions for Correct trials. Importantly, changes in the proportion of mu oscillations detected were not significant [$p >$

.1]. These results confirm the patterns of activity observed in the P_{epiosde} plots, depicting more theta and alpha oscillatory activity detected from Fz and Pz, respectively, as a function of accuracy.

Relationships between questionnaires

TAMlw

Relating the hand-imagery questionnaire to TAMlw produced a moderate correlation, indicating that both of these questionnaires elicit some common cognitive process to perform the task. [$r(24) = .48, p < .05$]. With this relationship corresponding to only 23% of overall shared variance (i.e., r^2), it suggests that different imagery strategies may be adopted by participants between the hand-imagery questionnaire and TAMlw. We performed partial correlations, such that the four FPIQ subscales and the MRT were partialled out, to control for relationships with these other questionnaires that could completely explain the relationship between TAMlw and the hand-imagery questionnaire. This produced a weaker, albeit significant correlation, eliminating the severity of a shared source of variability [$r_p(20) = .41, p < .05$].

FPIQ and MRT

We correlated the hand-imagery questionnaire to each of the four subscales of the FPIQ (Table 2). Partial correlations were performed to determine the degree to which the shared covariance between the subscales of the FPIQ explained the relationship to the hand-imagery questionnaire. Specifically, relating the hand-imagery questionnaire to a specific subscale of the FPIQ (e.g., Position) would involve partialling out the remaining subscales (in this example, Kinesthetic, Object, and Action would be partialled out). The partial correlation results were not

significant [Position $r_p(21) = .343, p = .086$; Kinesthetic $r_p(21) = .298, p = .139$; Object $r_p(21) = .311, p = .122$; Action $r_p(21) = .280, p = .166$] Observing the FPIQ subscales highly covarying with each other replicates previous findings (Donoff et al., 2018).

The hand-imagery questionnaire was related to the MRT, to determine the degree to which these two tasks share a common source of variability [$r(24) = .353, p > .05$]. The absence of a significant correlation between the hand-imagery questionnaire and MRT suggests that different components of spatial imagery are being attended to (form versus movement) to successfully complete each task. (Insert Table 2 here).

EHI

An Item-laterality difference score was calculated by subtracting Left-handed scores from Right-handed scores, providing an index of right-hand performance. This was related with the EHI LQ scores (also an index of right-handedness). No significant correlation was observed [$r(24) = .319, p > .05$].

Discussion

The present study sought to observe the electrophysiology associated with imagining hand movements. Specifically, can we detect lateralized mu suppression while participants complete the hand-version of TAMI, indicative that this objective measure induces motor imagery processes. The design of this study was chosen to replicate and extend the findings of Lambert et al. (In-prep), in which mu-suppression was observed over motor regions during successful whole-body movement imagery. Here, the inclusion of both right- and left-handed participants completing a hand-version of TAMI led to predictions of lateralized mu suppression

during successful trials. The hand-imagery questionnaire evoked significant increases in alpha oscillations detected over parietal regions (Pz) during successful trials over error trials, as well as increased theta over frontal regions (Fz) during successful trials over error trials. This pattern of activation suggests different components of spatial imagery were attended to in order to successfully complete the questionnaire (Kozhevnikov, Kosslyn, & Shepard, 2005). Specifically, the significant increase of frontal-midline theta oscillations indicates that the participant was engaging in a more complex task requiring heightened concentration (Fellrath et al., 2016). Combined with a simultaneous increase in posterior alpha, this pattern of results suggests the dorsal fronto-parietal network (dFPN) may have played a role in internally directing the attention of the participants to maintaining and updating spatial representations of overall hand form, or finger locations, as opposed to simulating the motor movement of the fingers. The moderate correlation between the hand-imagery questionnaire and the TAMIW, as well as the lack of significant partial correlations with the FPIQ subscales and EHI taken together suggest the computerized hand-imagery questionnaire may have encouraged spatial imagery, as opposed to motor imagery, to successfully complete the task. No behavioral interaction was observed between an individual's handedness and the type of trial (right- or left-hand questions). Further, no significant suppression of mu oscillations was detected during successful trials.

There are several important differences between the original TAMI and hand-version that may significantly alter how the task is cognitively performed. Where TAMI used instructions for gross, whole-body movements, the hand-imagery questionnaire required participants to imagine fine finger-movements. The difference in absolute distance in finger- versus limb-movements is apparent. Mental rotation tasks, among others, have confirmed that varying the degree of rotation or distance travelled transfers to the relative amount of time a person spends mentally simulating

the movement (Shepard & Metzler, 1971; Pinker & Kosslyn, 1978; Rinck & Denis, 2004). From a purely quantitative perspective, the reduced proportion of time a participant simulates a finger movement compared to a limb could very well reduce effects of mu-suppression related motor activity from being observed. Similarly, the difference in spatial scale could also play a role. It could be harder to imagine the movements of smaller body parts that are closer together (i.e., the fingers) vs. much larger body parts such as an entire arm or leg. There are numerous studies investigating the neural correlates of imagined-hand movements (Lotze et al., 1999; Muthukumaraswamy, Johnson, & McNair, 2004; Pfurscheller et al., 2006; Nam et al., 2011; Formaggio et al., 2015). Many of these extant studies that report mu-suppression often are limited to hand rotations, as well as reaching and grasping actions that both have a longer duration of mentally simulated movement, as well as introduce goal-oriented action (Balconi, Cortesi, & Crivelli, 2017). Both the TAMI and hand-version induce intransitive (non-goal-/tool-oriented) movements, making this factor insufficient at explaining the lack of mu-suppression observed here. Further, extant studies on hand-movement imagery often employ a self-paced paradigm, which would potentially reduce the difficulty of the task. Though not recorded over central electrode sites, it has been demonstrated that as imagery difficulty increases, there is a decrease in alpha ERD over occipital sites O1 and O2 (Igasaki, Takemoto, & Sakamoto, 2018). Specifically, participants were instructed to imagine the single flexion of the right index finger either with kinesthetic motor imagery (KMI; including the sensations involved with the movement) or visual motor imagery (VMI; simulating only the visual movement) instructions. Participants who felt the motor imagery was easy displayed greater alpha ERD for both KMI and VMI, which resembled the alpha ERD during movement execution. Participants who reported motor imagery to be highly difficult produced less alpha ERD during KMI instructions compared

to alpha ERD under VMI instructions. The pattern of these results suggests that if a task is difficult and increases the cognitive load on the participant, less ERD will be observed in areas unnecessary for the completion of the task. This makes sense in light of the results found here, as both mu and alpha oscillations reflect inhibitory processes. It is possible that the hand-imagery questionnaire presented a difficult task that did not required simulations of motor movement. Increased concentration accompanied by internally directed attention may have resulted in continued inhibition over central electrode sites, to enable other areas specific to the task (spatial processing, working memory, etc.) to be elicited. Further research on the effects of imagery difficulty should be performed to better understand this potential factor of mental imagery.

One factor differentiating the TAMI with the hand-imagery questionnaire is the difference in cognitive load. Situations forcing a higher cognitive load involve greater degrees of freedom/number of analyses in order to complete the task. Greater degrees of freedom mean there are more variables the cognitive model needs to consider, which reportedly recruits greater cognitive resources (Krause et al., 2000; Jensen & Tesche, 2002; Onton, Delorme, & Makeig, 2005). Specifically, increased frontal-midline theta has been observed to increase parametrically as the number of items in working memory is increased (Krause et al., 2000). The present results of increased frontal-midline theta and posterior parietal alpha suggests that the hand-imagery questionnaire may have recruited spatial working memory processes over movement imagery. This pattern of activity is supported by studies observing these regions activated during working memory tasks, as Scheeringa et al. (2009) replicated findings of parametric changes in oscillatory activity in frontal theta and posterior parietal alpha as a function of working memory load on the Sternberg task using simultaneous EEG and fMRI. The Sternberg task requires participants to hold strings of numbers of increasing length in working memory. It is thought that

the increase in posterior alpha serves to inhibit processes that would otherwise disturb the contents of working memory (Scheeringa et al., 2009; Proskovec et al., 2018).

Where TAMI appeared to elicit movement imagery, the hand-imagery questionnaire appeared to elicit spatial working memory. TAMI used a smaller set of possible actions compared to the hand-imagery questionnaire. Hand-movement instructions included crossing different digits in-front or behind one another, or curling a finger down versus pointing a finger either perpendicular/parallel to the plane of the palm. Further, early instructions to rotate the hand 90 degrees or 180 degrees drastically increases the number and pattern of spatial relationships a participant has to consider, making the order of instructions a factor that is absent in the TAMI. This increased complexity and necessity to keep order in mind may have forced participants to utilize working memory instead of mentally simulating the movement of each finger. Statically ‘stitching’ together the sequential finger-movement commands visuospatially, holding them in working memory, and manipulating them in a more abstract fashion could be more effective at correctly answering the questions, as opposed to simulating the finger motion of each instruction. EEG studies have observed the elicitation of frontal theta and posterior parietal alpha associated with internally directed attention when performing tasks that require assessment and modification of spatial features (Lenartowicz et al., 2016; Proskovec et al., 2018). Mentally simulating the relative positions of the fingers to each other resembles the process of assessing and manipulating the relative positions of features of an abstract object.

The computerized version of the hand-imagery questionnaire differs from the pencil-and-paper version used in Donoff et al. (2018) with respect to the pacing of mental imagery. In Donoff et al. (2018), participants could spend as much time as they liked reading the instructions, following a self-paced design. The present study presented instructions automatically, in six

second intervals. In both studies, participants were not allowed to review the finger-movement instructions once the response page appeared (was flipped to). As previously mentioned with regard to the extant hand-imagery studies, the difference in time allotted to initially imagine the hand-movement instructions alone could influence whether a participant simulates spatial representations of general form and location, or of movement information, such as direction and velocity. Given a time constraint, participants may focus on encoding the relative positions of the fingers in relation to each other in a static image, as opposed to mentally simulating the short and subtle movements involved, as the latter is not necessary to accurately complete the task. Though all versions of TAMI instructed participants to imagine themselves perform the actions, there was no inclusion of a control to ensure participants are mentally simulating the action, as opposed to simulating the static representations of the relative positions of the limbs. In future studies seeking to measure motor imagery, providing a control task to ensure participants are imagining the information pertinent to motor movements would provide assurance that simulations of static spatial representations are not being adopted. One approach to accomplish this would be to include catch-trials, such that obstacles are present in the path of a particular finger-movement instruction. These catch-trials would place the initial hand position image against a peg-board, with pegs positioned at different locations across catch-trials. The important element would be the position of these pegs blocking the trajectory of certain finger movements, as opposed to blocking the final state of each instruction. This would ensure participants are imagining the movement and path of a finger/hand movement, instead of the final states stitched together.

Another difference in the computerized hand-imagery questionnaire is the absence of the Functionally-involved trials that appeared in the pencil-and-paper version. These trials were

omitted in the present study to replicate the original TAMI, both using intransitive movements. The hand-dominance effect reported in Donoff et al. (2018) could have been produced by a priming effect of the Functionally-involved trials. Because the Functionally-involved (transitive) and Isolated-movement (intransitive) trials were interleaved, it is possible that the transitive, object-oriented trials induced pre-motor priming during the intransitive trials, driving a hand-dominance effect. Follow-up investigations should block these two types of trials, to control for the possibility of priming effects, and test whether this novel questionnaire of imagined transitive movements evokes more motoric regions than intransitive, which we would expect from previous studies demonstrating that the perception of objects/tools elicits motor simulations (Järveläinen, Schürmann, & Hari, 2004; Nicola et al., 2008; Rueschemeyer et al., 2010; Collette et al., 2016; Madan, Chen, & Singhal, 2016; Mollo, Pulvermüller, & Hauk, 2016; Grisoni, Dreyer, & Pulvermüller, 2016).

Hands themselves are a very goal-oriented part of our bodies. They are used to convey information, as well as interact with a wide variety of objects and tools. The combination of short, fleeting finger movements that are intransitive encompasses a type of action that we rarely experience. Where we do rotate our bodies and lift particular limbs on a daily basis, we rarely cross our fingers in conjunction with curling a pinky finger down to the palm, while rotating our hand 180 degrees. There is evidence suggesting that visuo-spatial processes can play a role in motor imagery associated with less object/goal-oriented action (Schulz et al., 2018). Specifically, grasping adjacent to an object induced visuospatial regions such as posterior parietal lobe and premotor cortex, whereas grasping an object only elicited motor regions. Looking at these results again from a purely experience-based perspective, there is less physical practice with grasping next to objects as opposed to grasping the object itself. The effect of embodied experience on

imagery ability (Conson, Mazzarella, & Trojano, 2011; Guillot, Moschberger, & Collet, 2013) and neural activity (Gerardin et al., 2000) has been investigated, depicting priming effects of explicit movement on motor imagery. Explicitly practicing the physical movements acts to provide a reference for future imagined movements, including the kinesthetic feedback associated with motor movements. Movements for which we are more experienced with have been shown to evoke more localized and efficient brain activity (Munte et al., 2002; Lotze et al., 2003). Our results support these findings, with the recruitment of both frontal and posterior parietal regions representing a more distributed state of processing compared to localized secondary motor cortex activity (Jäncke et al., 2000). Requiring participants to imagine these uncommon, intransitive hand movements may have required more cognitive resources than imagining transitive hand movements, resulting in the adoption of spatial working to assist with the task. Future investigations could include blocks of similar, explicit hand-movement trials to provide a prime for participants, which would enhance the vividness and adoption of using movement imagery. The inclusion of anatomically impossible trials could enhance the recruitment of motor regions, as Ebersbach and Krüger (2017) demonstrated participants had better arm laterality judgements for human figures in possible versus impossible positions.

Taken together, the pattern of results depicting increased frontal-midline theta and posterior parietal alpha oscillations for successful trials indicates that the computerized version of the hand-imagery questionnaire may have induced other cognitive processes, like spatial working memory. Differences between the present study and TAMI include scale of movement and required cognitive load. Distinctions to the pencil-and-paper version appearing in Donoff et al. (2018) include object/goal-oriented priming and pacing of imagery instructions. Going forward, two versions of the hand-imagery questionnaire could be developed to manipulate

which type of mental simulation (movement versus spatial) is being utilized. This could be achieved by allowing self-paced imagery instruction steps to reduce the necessity of working memory, as well as include explicit hand-movement blocks to prime the participants with physical representations of the actions.

References

- Bakeman, R. (2005). Recommended effect size statistics for repeated measures designs. *Behavior Research Methods, 37*(3), 379-384.
- Balconi, M., Cortesi, L., & Crivelli, D. (2017). Motor planning and performance in transitive and intransitive gesture execution and imagination: Does EEG (RP) activity predict hemodynamic (fNIRS) response? *Neuroscience Letters, 648*, 59–65.
- Berryhill, M. E., & Olson, I. R. (2008). Is the posterior parietal lobe involved in working memory retrieval? Evidence from patients with bilateral parietal lobe damage: What is the Parietal Lobe Contribution to Human Memory? *Neuropsychologia, 46*(7), 1775.
- Blajenkova, O., Kozhevnikov, M., & Motes, M. A. (2006). Object-spatial imagery: A new self-report imagery questionnaire. *Applied Cognitive Psychology, 20*(2), 239.
- Callow, N. & Hardy, L. (2004). The relationship between the use of kinaesthetic imagery and different visual imagery perspectives. *Journal Of Sports Sciences, 22*(2), 167-177.
- Collette, C., Bonnotte, I., Jacquemont, C., Kalénine, S., & Bartolo, A. (2016). The development of object function and manipulation knowledge: Evidence from a semantic priming study. *Frontiers in Psychology, 7*.
- Conson, M., Mazzarella, E., & Trojano, L. (2011). Self-touch affects motor imagery: a study on posture interference effect. *Experimental Brain Research, 215*(2), 115-122.

- Del Gratta, C., Di Matteo, R., De Nicola, A., Ferretti, A., Tartaro, A., Bonomo, L., ... Belardinelli, M. (2001). Sensory image generation: a comparison between different sensory modalities with fMRI. *Neuroimage*, *13*(6), 394.
- Dijkstra, N., Bosch, S. E., & van Gerven, M. A. J. (2019). Shared neural mechanisms of visual perception and imagery. *Trends in Cognitive Sciences*, *23*(5), 423–434.
- Ebersbach, M., & Krüger, M. (2017). Let's twist again! Embodiment effects in spatial judgments on human figures rotated along a vertical axis. *Journal of Cognitive Psychology*, *29*(8), 963–976.
- Electrical Geodesics, Inc. (2006). NetStation Waveform Tools Technical Manual (Tech. Rep. S-MAN-200-WTFR-001). Eugene, OR: EGI.
- Farah, M. J., Hammond, K. M., Levine, D. N., & Calvanio, R. (1988). Visual and spatial mental imagery: dissociable systems of representation. *Cognitive Psychology*, *(4)*, 439.
- Fellrath, J., Mottaz, A., Schnider, A., Guggisberg, A. G., & Ptak, R. (2016). Theta-band functional connectivity in the dorsal fronto-parietal network predicts goal-directed attention. *Neuropsychologia*, *92*, 20–30.
- Fiehler, K., & Roesker, F. (2010). Plasticity of multisensory dorsal stream functions: Evidence from congenitally blind and sighted adults. *Restorative Neurology And Neuroscience*, *28*(2), 193–205.
- Filgueiras, A., Quintas Conde, E. F., & Hall, C. R. (2018). The neural basis of kinesthetic and visual imagery in sports: an ALE meta-analysis. *Brain Imaging and Behavior*, *12*(5), 1513–1523.

- Gerardin, E., Sirigu, A., Lehericy, S., Poline, J.B., Gaymard, B., Marsault, C., Agid, Y., & Le Bihan, D. (2000). Partially Overlapping Neural Networks for Real and Imagined Hand Movements. *Cerebral Cortex*, *10*(11), 1093-1104.
- Grisoni, L., Dreyer, F. R., & Pulvermüller, F. (2016). Somatotopic semantic priming and prediction in the motor system. *Cerebral Cortex*, *26*(5), 2353-2366.
- Guillot, A., Moschberger, K., & Collet, C. (2013). Coupling movement with imagery as a new perspective for motor imagery practice. *Behavioral & Brain Functions*, *9*(1), 1–8.
- Heremans, E., Feys, P., Nieuwboer, A., Vercruyse, S., Vandenberghe, W., Sharma, N., & Helsen, W. (2011). Motor imagery ability in patients with early- and mid-stage Parkinson disease. *Neurorehabilitation and Neural Repair*, *25*(2), 168–177.
- Igasaki, T., Takemoto, J., & Sakamoto, K. (2018). Relationship between kinesthetic/visual motor imagery difficulty and event-related desynchronization/synchronization. *IEEE Engineering in Medicine and Biology Society*, 1911-1914.
- Järveläinen, J., Schürmann, M., & Hari, R. (2004). Activation of the human primary motor cortex during observation of tool use. *Neuroimage*, *23*(1), 187-192.
- Jeannerod, M. (1994). The representing brain: Neural correlates of motor intention and imagery. *Behavioral And Brain Sciences*, *17*(02), 187.
- Just, M., Cherkassky, V., Aryal, S., & Mitchell, T. (2010). A neurosemantic theory of concrete noun representation based on the underlying brain codes. *PLoS ONE*, *5*(1), e8622.

- Kozhevnikov, M., Kosslyn, S., & Shepard, J. (2005). Spatial versus object visualizers: A new characterization of visual cognitive style. *Memory & Cognition*, (4), 710.
- Krause, C.M., Sillanmaki, L., Koivisto, M., Saarela, C., Haggqvist, A., Laine, M., Hamalainen, H., 2000. The effects of memory load on event-related EEG desynchronization and synchronization. *Clinical Neurophysiology*. 111, 2071–2078.
- Lambert, K., Chen, Y., Madan, C., & Singhal, A. (In-prep). The neural correlates of movement imagery: mu rhythm reflects imagery success and ability.
- Lebon, F., Horn, U., Domin, M., & Lotze, M. (2018). Motor imagery training: Kinesthetic imagery strategy and inferior parietal fMRI activation. *Human Brain Mapping*, 39(4), 1805–1813.
- Lenartowicz, A., Lu, S., Rodriguez, C., Lau, E. P., Walshaw, P. D., McCracken, J. T., ... Loo, S. K. (2016). Alpha desynchronization and frontoparietal connectivity during spatial working memory encoding deficits in ADHD: A simultaneous EEGfMRI study. *NeuroImage: Clinical*, 11, 210–223.
- Lindstrom, M.J., & Bates, D.M. (1988). Newton-Raphson and EM algorithms for linear mixed-effects models for repeated-measures data. *Journal of the American Statistical Association*, 83, 1014–1022.
- Lotze, M., Montoya, P., Erb, M., Hülsmann, E., Flor, H., Klose, U., ... Grodd, W. (1999). Activation of cortical and cerebellar motor areas during executed and imagined hand movements: an fMRI study. *Journal Of Cognitive Neuroscience*, 11(5), 491–501.

- Lotze, M., Scheler, G., Tan, H. R., Braun, C., and Birbaumer, N. (2003). The musician's brain: functional imaging of amateurs and professionals during performance and imagery. *Neuroimage* 20, 1817–1829.
- Madan, C.R., & Singhal, A. (2012). Motor imagery and higher-level cognition: Four hurdles before research can sprint forward. *Cognitive Processing*, 13(3), 211-229.
- Madan, C.R., & Singhal, A. (2013). Introducing TAMI: An objective test of ability in movement imagery. *Journal of Motor Behavior*, 45(2), 153-166.
- Madan, C.R., & Singhal, A. (2014). Improving the TAMI for use with athletes. *Journal of Sports Sciences*, 32(14), 1351-1356.
- Madan, C., Chen, Y., & Singhal, A. (2016). ERPs differentially reflect automatic and deliberate processing of the functional manipulability of objects. *Frontiers In Human Neuroscience*, 10, 360.
- Martin, S., Mikutta, C., Leonard, M. K., Hungate, D., Koelsch, S., Shamma, S., ... Pasley, B. N. (2018). Neural encoding of auditory features during music perception and imagery. *Cerebral Cortex*, 28(12), 4222–4233.
- McAvinue, L. P., & Robertson, I. H. (2007). Measuring Visual Imagery Ability: A Review. *Imagination, Cognition and Personality*, 26(3), 191–211.
- McKelvie, S. J. (1995). The VVIQ as a psychometric test of individual differences in visual imagery vividness: a critical quantitative review and plea for direction. *Journal of Mental Imagery*, 19, 1–106.

- Mollo, G., Pulvermüller, F., & Hauk, O. (2016). Movement priming of EEG/MEG brain responses for action-words characterizes the link between language and action. *Cortex*, *74*, 262–276.
- Munte, T. F., Altenmüller, E., and Jancke, L. (2002). The musician's brain as a model of neuroplasticity. *Nature Reviews Neuroscience*, *3*, 473–478.
- Muthukumaraswamy, S., Johnson, B., & McNair, N. (2004). Mu rhythm modulation during observation of an object-directed grasp. *Cognitive Brain Research*, *19*(2), 195-201.
- Nicola, C., Francesca, B., Stefano F., C., Daniela, P., Andrea, F., Giovanni, B., ... Tim, S. (2008). The Different Neural Correlates of Action and Functional Knowledge in Semantic Memory: An fMRI Study. *Cerebral Cortex*, (4), 740.
- Oldfield, R. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*(1), 97-113.
- Onton, J., Delorme, A., & Makeig, S. (2005). Frontal midline EEG dynamics during working memory. *Neuroimage*, *27*(2), 341–356.
- Palmiero, M., Olivetti Belardinelli, M., Nardo, D., Di Matteo, R., D'Ausilio, A., Sestieri, C., & Romani, G. L. (2009). Mental imagery generation in different modalities activates sensory-motor areas. *Cognitive Processing*, *10*(2), 268–271.

- Pfurtscheller, G., Brunner, C., Schlögl, A., & Lopes da Silva, F. H. (2006). Mu rhythm (de)synchronization and EEG single-trial classification of different motor imagery tasks. *Neuroimage*, *31*(1), 153–159.
- 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*(10), e0198051.
- Pinker, S., & Kosslyn, S. M. (1978). The representation and manipulation of three-dimensional space in mental images. *Journal of Mental Imagery*, *2*(1), 69-84.
- Porro, C., Francescato, M., Cettolo, V., Baraldi, P., & Diamond, M. (1996). Primary motor cortex activity during motor performance and motor imagery: A fMRI study. *Neuroimage*, *3*(3), S214.
- Proskovec, A. L., Wiesman, A. I., Heinrichs-Graham, E., & Wilson, T. W. (2018). Beta oscillatory dynamics in the prefrontal and superior temporal cortices predict spatial working memory Performance. *Scientific Reports*, *8*(1), 8488.
- Pruitt, T. A., Halpern, A. R., & Pfordresher, P. Q. (2019). Covert singing in anticipatory auditory imagery. *Psychophysiology*, *56*(3), e13297.
- Psychology Software Tools, Inc. [E-Prime 2.0]. (2012). Retrieved from <https://www.pstnet.com>.
- Ptak, R., Schnider, A., & Fellrath, J. (2017). The Dorsal Frontoparietal Network: A core system for emulated action. *Trends in Cognitive Sciences*, *21*(8), 589–599.

- Rinck, M., & Denis, M. (2004). The metrics of spatial distance traversed during mental imagery. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 30(6), 1211-1218.
- Rueschemeyer, S., van Rooij, D., Lindemann, O., Willems, R., & Bekkering, H. (2010). The function of words: Distinct neural correlates for words denoting differently manipulable objects. *Journal Of Cognitive Neuroscience*, 22(8), 1844-1851.
- Sabaté, M., González, B., & Rodríguez, M. (2004). Brain lateralization of motor imagery: motor planning asymmetry as a cause of movement lateralization. *Neuropsychologia*, 42(8), 1041-1049.
- Sack, A. T., Jacobs, C., De Martino, F., Staeren, N., Goebel, R., & Formisano, E. (2008). Dynamic premotor-to-parietal interactions during spatial imagery. *Journal of Neuroscience*, 28(34), 8417–8429.
- Schulz, L., Ischebeck, A., Wriessnegger, S. C., Steyrl, D., & Mueller-Putz, G. R. (2018). Action affordances and visuo-spatial complexity in motor imagery: An fMRI study. *Brain and Cognition*, 124, 37–46.
- Sirigu, A., and Duhamel, J. (2001). Motor and visual imagery as two complementary but neurally dissociable mental processes. *Journal of Cognitive Neuroscience*, 13(7), 910-919.
- Shepard, R. N., & Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science*, 171, 701–703.

- Taube, W., Mouthon, M., Leukel, C., Hoogewoud, H. M., Annoni, J. M., & Keller, M. (2015). Brain activity during observation and motor imagery of different balance tasks: an fMRI study. *Cortex*, *64*, 102-114.
- Toriyama, H., Ushiba, J., & Ushiyama, J. (2018). Subjective vividness of kinesthetic motor imagery is associated with the similarity in magnitude of sensorimotor event-related desynchronization between motor execution and motor imagery. *Frontiers in human neuroscience*, *12*, 295.
- Willems, R. M., Toni, I., Hagoort, P., & Casasanto, D. (2009). Body-specific motor imagery of hand actions: neural evidence from right- and left-handers. *Frontiers In Human Neuroscience*, *3*, 39.
- Williams, S. E., Cumming, J., & Edwards, M. G. (2011). The functional equivalence between movement imagery, observation, and execution influences imagery ability. *Research Quarterly for Exercise and Sport*, *82*(3), 555-564.
- Wilson, V., Dikman, Z., Bird, E., Williams, J., Schwartz, G., Harmison, R., & Shaw-Thornton, L. (2016). EEG topographic mapping of visual and kinesthetic imagery in swimmers. *Applied Psychophysiology & Biofeedback*, *41*(1), 121-127.
- Yang, J., and Shu, H. (2013). Passive reading and motor imagery about hand actions and tool-use actions: an fMRI study. *Experimental Brain Research*, *232*(2), 453-467.

Table 1. Descriptive statistics of raw scores for all mental imagery measures and subscales.

	<i>M</i>	<i>SD</i>	Possible range	Observed range
Hand-imagery	14.760	4.123	0 – 20	3 – 20
TAMIw	16.933	3.223	0 – 24	5 – 24
FPIQ-Kinesthetic	8.971	1.442	0 – 12	4 – 12
FPIQ-Position	10.657	1.917	0 – 12	6 – 12
FPIQ-Action	10.214	1.554	0 – 12	4 – 12
FPIQ-Object	10.510	1.349	0 – 12	5 – 12
MRT	17.257	5.536	0 – 23	4 – 23

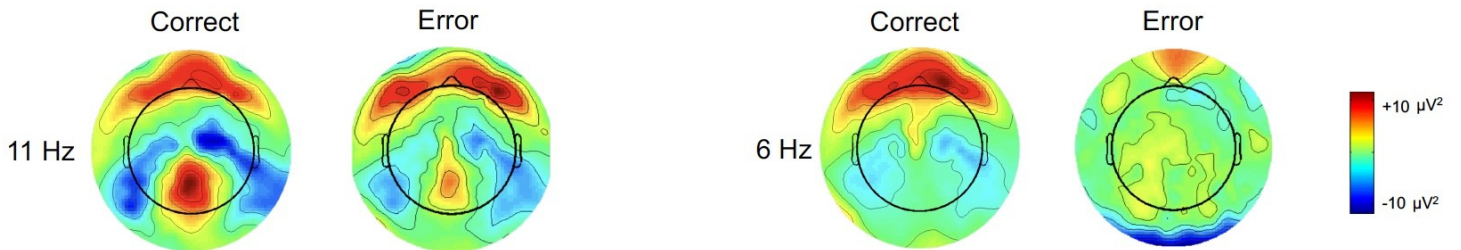
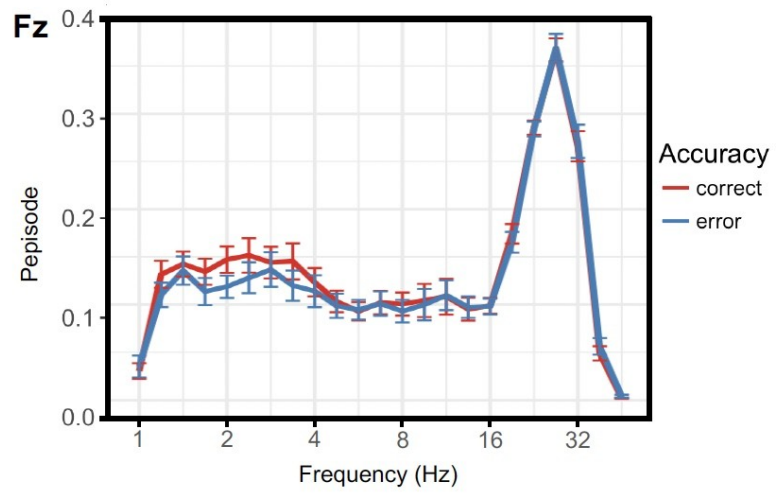
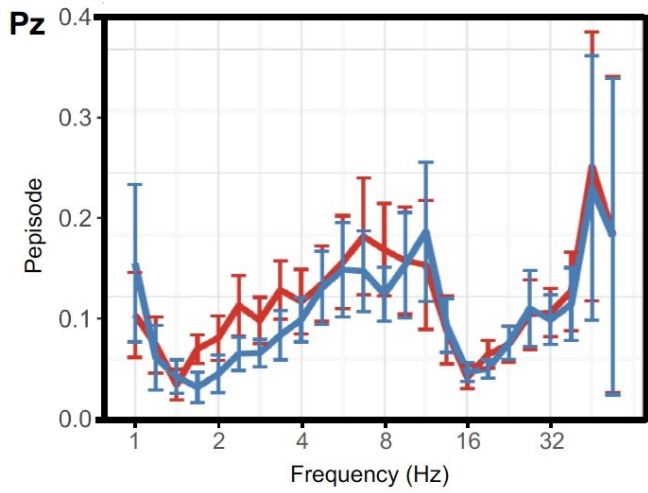
Table 2. Correlations (*r*) between the Hand-imagery Questionnaire and the TAMIw, FPIQ subscales, MRT and EHI.

Hand-imagery questionnaire	
<i>r</i>-coefficients	
TAMIw	.482*
FPIQ-Kinesthetic	.257
FPIQ-Position	.465*
FPIQ-Action	.325
FPIQ-Object	.422*
MRT	.353
EHI	.319

* = $p < .05$.

Figure 1: Proportion of oscillatory activity detected as a function of frequency at Pz and Fz sites.

Figure 2: Topographic maps of activity in the theta (4-7 Hz) and alpha (8-13 Hz) frequency bands for both Correct and Error trials.



Chapter 4:

Discussion

Discussion

The work presented in this thesis was intended to both replicate and extend findings in the motor imagery literature, which largely posit the involvement of overlapping motor processes in both real and simulated action (Jeannerod, 1994; Lotze et al., 1999; González, & Rodríguez, 2004; Formaggio et al., 2015). Chapters 2 and 3 describe two studies that utilized a hand-version of a novel objective measure of motor imagery (TAMI), following the assumption that individuals vary in their ability to form mental images (Hishitani, 2009; Conson, Mazzarella, & Trojano, 2011; Guillot, Moschberger, & Collet, 2013). Results from Chapter 2 depicted a right-handedness effect in right-handed participants, such that their performance was greater when imagining dominant hand versus non-dominant hand movements. These results are consistent with the notion that motor imagery requires the elicitation of similar motor regions that are involved in planning real motor movements. In Chapter 3, the intent was to expand on the findings in Chapter 2, and observe the mu suppression effect observed at the onset and duration of real and simulated action (Pfurtscheller et al., 2006; Nam et al., 2011). Results from Chapter 3 showed statistically significant increases in frontal-midline theta and posterior-alpha power on correct trials, indicating that processes associated with increased concentration and internally directed attention were useful for the participant to successfully perform the computerized hand-version of the task.

Mental imagery denotes an incredibly vast and deep array of sub-component processes (McAvinue & Robertson, 2006) aggregated to form this seemingly unitary cognitive function. Due to its disparate composition, the demand for imagery measures to target specific facets of mental imagery grows. The efficacy of mental health (Moscovitch, Chiupkia, & Gavric, 2013; Schweta & Deepak, 2015; Murphy et al., 2017), neuroprosthetic (Kondo et al., 2015; Liu et al.,

2017), sports training (Bouhika et al., 2016; Kaminsky & Vereksa, 2017), and other neurorehabilitation programs utilizing mental imagery depends on both our increased understanding, and ability to induce and measure these specific forms of mental imagery. For example, learning which external environments and internal mental states enhance the ease in which a person can simulate motor movements (in the case for rehabilitating motor deficits or enhancing sport performance), would provide more effective rehab and performance tools. The results from the work presented here illustrate the importance of designing tasks that control and manipulate factors that may influence whether motor or spatial imagery is being measured. Participants complete objective measures of mental imagery in a means that yields accurate results, and those means may not align with the processes investigators are attempting to measure. Even with explicit instructions for participants, the reliance on accuracy scores as a control for task compliance is not a catch-all solution. Other steps are needed to restrict the mental imagery process employed by the participant to the one in question (i.e. motor, spatial, visual, etc.).

One factor to consider when designing an imagery task is the complexity or difficulty of the imagery task. Studies have found task difficulty can modulate the reported imagery vividness, such that tasks that increase working memory demand resulted in self-reports of reduced imagery vividness (Engelhard, van den Hout, & Smeets, 2011). Further, it has been found that as imagery vividness varies, the type of neural network elicited also varies (Logie et al., 2011). Specifically, proficient imagers utilize more sensory cortex regions, associated with simulating more sensorimotor detail, whereas non-proficient imagers utilize the fronto-parietal network, associated with more abstract forms of spatial representation. Therefore, designing tasks that provide high cognitive-load demands may force participants to use less vivid spatial

imagery, as well as incorporate working memory processes. Task difficulty may arise in various forms, either by a large set of potential actions/stimuli to imagine, the degree of detail in describing an action/visual stimulus, as well as the time allotted to perform the imagery process. Where an imagery task is situated on any of these dimensions will influence the cognitive process employed by the participant. If investigators wish to induce and measure motor imagery, they must ensure their task provides the conditions in which motor imagery can arise and be necessary for the successful completion of the task (Zacks, 2008). Indeed, the activation of motor cortex regions during mental imagery of other modalities has been observed (Halpern et al., 2004; Palmiero et al., 2009; Winlove et al., 2018), however if task conditions change, other regions will take over to assist in proficiently completing the task. For example, spatial imagery tasks that do not provide sufficient conditions for motor incorporation have been found to engage the parietal lobe, suggested to play a role in spatial-manipulation processes (Thompson et al., 2009). More work needs to be done to specify these cognitive process transition points as a function of cognitive load. For example, the pacing of a task may influence whether highly-vivid imagery, or more abstract forms of spatial working memory are utilized by the participant.

Another factor that can influence whether motoric movement information is being simulated by a participant is the scale of stimuli. Here, scale refers to the number of objects or parts of objects emphasized in the stimuli or question. This property of stimuli can be manipulated by changing the number of objects appearing in a question/stimulus, or increasing the resolution of detail, necessitating the creation of more items in working memory. Manipulations of this sort probe participants to assess either local (e.g., color, texture, brightness) or global (e.g., relative distance, relative size, movement) characteristics by virtue of orienting a participant's attention (Kozhevnikov, Blazhenkova, & Becker, 2010). The two forms of imagery,

object and spatial, have been found to differentially rely on this stimulus property of scale. One study demonstrated that object imagery loads on the dimension restricted to pictorial qualities and schema involving one object, whereas spatial imagery loads on the dimension of detailed 3D structures involving multiple objects or parts of objects (Blazhenkova et al., 2016). Items that involve the processing of multiple components leads participants to assess relational information, whereas items that direct attention towards a single object recruit pictorial information. Research going forward should be mindful of the potential factors influencing whether their task promotes simulations of spatial representations of form, location, and relative position versus direction, velocity, and kinesthetic movement information.

The work presented here was motivated to continue the development and assessment of a novel objective measure of movement imagery. The results from the two studies indicates the novel task involving hand imagery is situated within these factors influencing the recruitment of movement information to complete the task, such that conditions for motor imagery were not entirely met. Though some motoric activation was observed over central electrode sites C3 and C4, it did not drive accuracy on the task. Patterns that suggest some motoric involvement include the greater variance in accuracy seen in left-handers compared to right-handers. Such a observation reflects the finding that left-handers present less functional asymmetry as right-handers, and therefore use their dominant hand less often than right-handers (Scharoun & Bryden, 2014). Instead, the combination of restricted time, high level of description, number of instructions, and lack of explicit practice suggests participants employed spatial imagery to successfully accomplish the task. Future versions of this objective measure should explicitly explore the effect of these factors, to both support the extant literature reporting their effects, as well as further develop this multiple-choice style task as a valid imagery measure. The first

investigation would seek to explicitly determine whether time constraints affect the employment of movement versus spatial working memory. To reduce the potential of priming effects, this manipulation would either be blocked or between subjects, such that trials would differ in terms of being self-paced, or time-restricted. Given the results from the present work, it would be predicted that self-paced trials would allow enough time to simulate the finger movements, enabling lateralized event-related desynchronizations (ERD) to be detected. Time-restricted trials, as appearing here, would discourage participants from simulating the movement, and instead, they would internally direct their attention to the spatial relationships between finger movement instructions, eliciting the frontoparietal regions involved with computing spatial representations. The observation of such time-restriction effects would provide preliminary evidence that highly detailed and complex imagery instructions, involving multiple objects or parts of objects, evokes spatial imagery in the absence of motor involvement. In a follow up study, manipulations on the degree of detail in finger movement instructions could further support this notion. Such a study entails predictions of interactions between the factor of Imagery time and Imagery detail, such that lateralized ERDs over motor cortex regions would be expected for trials that are self-paced, and with low detail, and become diminished under conditions of self-pacing and high-detail.

If, instead, motor involvement is still not shown to drive performance, and no significant lateralized ERDs are observed, the factor of familiarity and experience should be investigated. Given the intransitive, or non-goal oriented nature of the finger movement instructions appearing here, it is possible that participants did not imagine the hand as their own, but rather as an abstract object in which they were performing spatial manipulations on. To test this, trials could vary in terms whether they are transitively or intransitively described. For example, the same

finger movement instruction could be presented in an intransitive fashion, as appears in the work presented here, ‘Curl your index, middle, ring, and pinky fingers down to the plane of your palm’, or in a transitive, goal-oriented fashion, ‘Form a fist, as if you were to punch a punching bag’. The transitive instruction contains contextual information that a participant would more readily recognize, and potentially assist in elicitation of motoric processes. Indeed, extant studies have found transitive, goal-oriented imagined hand actions maximally elicit motoric regions compared to intransitive, abstract hand movements (Balconi, Cortesi, & Crivelli, 2017). Alternatively, explicit movement practice trials could be incorporated to help prime the motor plans associated with these finger movements (Guillot, Moschberger, & Collet, 2013). There is also evidence showing that the physical states of the hand can influence subsequent imagery processes. During a hand laterality judgement task, the physical orientation of a participant’s hand during imagery processes facilitated both the behavioral and electrophysiological activity associated with judging what would typically be a more difficult hand laterality judgement (Jongsma et al., 2013). Incorporating these explicit hand-movement trials would likely enhance the degree to which participants involve motoric processes. Future investigations would also benefit from collecting participants’ self-reports on the frame of reference they utilized to complete the task. These responses could be used to relate with the accuracy on the hand-movement questionnaire, as well as with the neural correlates associated with the degree of motor or spatial processing.

The ability to differentiate and understand the factors that dictate whether static properties of form, location, and relative position versus movement information are evoked experimentally will provide invaluable information for both a more fundamental understanding of the multifaceted nature of mental imagery, as well as improved control and efficacy of brain-

computer interface systems and neurorehabilitation programs. The degree to which mental imagery is involved in other cognitive processes is an outstanding question, and is one which may lead to significant advances in our ability to explain other adaptive and maladaptive behaviors.

Bibliography

- Alipour, A., Aerab-sheybani, K., & Akhondy, N. (2012). Effects of handedness and depth of processing on the explicit and implicit memory. *Procedia - Social And Behavioral Sciences*, 32, 29-33.
- Ankerst, M., Breunig, M., Kriegel, H., & Sander, J. (1999). OPTICS. *ACM SIGMOD Record*, 28(2), 49-60.
- Bakeman, R. (2005). Recommended effect size statistics for repeated measures designs. *Behavior Research Methods*, 37(3), 379-384.
- Balconi, M., & Cortesi, L. (2016). Brain Activity (fNIRS) in Control State Differs from the Execution and Observation of Object-Related and Object-Unrelated Actions. *Journal of Motor Behavior*, 48(4), 289–296.
- Balconi, M., Cortesi, L., & Crivelli, D. (2017). Motor planning and performance in transitive and intransitive gesture execution and imagination: Does EEG (RP) activity predict hemodynamic (fNIRS) response? *Neuroscience Letters*, 648, 59–65.
- Barsalou, L. (2008). Grounded Cognition. *Annual Review of Psychology*, 59(1), 617-645.
- Barlett, C. P., & Brannon, L. A. (2006). “If only...”: the role of visual imagery in counterfactual thinking. *Imagination, Cognition and Personality*, 26(1), 87-100.

- Beisteiner, R., Hollinger, P., Lindinger, G., Lang, W., & Berthoz, A. (1995). Mental representations of movements. Brain potentials associated with imagination of hand movements. *Electroencephalography and Clinical Neurophysiology*, (2), 183.
- Bensafi, M., Tillmann, B., Poncelet, J., Przybylski, L., & Rouby, C. (2013). Olfactory and gustatory mental imagery: modulation by sensory experience and comparison to auditory mental imagery. In *Multisensory imagery*, 77-91.
- Berryhill, M. E., & Olson, I. R. (2008). Is the posterior parietal lobe involved in working memory retrieval? Evidence from patients with bilateral parietal lobe damage: What is the Parietal Lobe Contribution to Human Memory? *Neuropsychologia*, (7), 1775.
- Betts, G. H. (1909). *The distribution and functions of mental imagery*. Teachers College, Columbia University.
- Blazhenkova, O. (2016). Vividness of Object and Spatial Imagery. *Perceptual & Motor Skills*, 122(2), 490–508.
- Blajenkova, O., Kozhevnikov, M., & Motes, M. A. (2006). Object-spatial imagery: A new self-report imagery questionnaire. *Applied Cognitive Psychology*, (2), 239.
- Bocchi, A., Carrieri, M., Lancia, S., Quaresima, V., & Piccardi, L. (2017). The key of the maze: The role of mental imagery and cognitive flexibility in navigational planning. *Neuroscience Letters*, 651, 146–150.

- Bouhika, E. J., Moussouami, S. I., Tsiama Portejoie, J. A., Bazaba Kayilou, J. M., Moyen, R., Mizere Mounghondo, M., ... Mbemba, F. (2016). Food Ration and Mental Training for the Improvement of the Free Throw Performance in Congolese Beginners Basketball Players. *Journal of Education and Training Studies*, 4(11), 119–124.
- Brodeur, M.B., Dionne-Dostie, E., Montreuil, T., & Lepage, M. (2010). The Bank of Standardized Stimuli (BOSS), a new set of 480 normative photos of objects to be used as visual stimuli in cognitive research. *PLoS ONE*, 5, e10773.
- Brodeur, M. B., Guérard, K., & Bouras M. (2014) Bank of Standardized Stimuli (BOSS) Phase II: 930 New Normative Photos. *PLoS ONE*, 9(9): e106953.
- Brookings, J., Wilson, G., & Swain, C. (1996). Psychophysiological responses to changes in workload during simulated air traffic control. *Biological Psychology*, 42(3), 361–377.
- Buccino, G., Binkofski, F., Fink, G., Fadiga, L., Fogassi, L., Gallese, V., et al. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *European Journal of Neuroscience*, 13(2), 400-404.
- Buzsaki, G. (2006). *Rhythms of the brain*. Oxford University Press.
- Callow, N. & Hardy, L. (2004). The relationship between the use of kinaesthetic imagery and different visual imagery perspectives. *Journal Of Sports Sciences*, 22(2), 167-177.
- Chao, L. & Martin, A. (2000). Representation of manipulable man-made objects in the dorsal stream. *Neuroimage*, 12(4), 478-484.

- Collette, C., Bonnotte, I., Jacquemont, C., Kalénine, S., & Bartolo, A. (2016). The Development of Object Function and Manipulation Knowledge: Evidence from a Semantic Priming Study. *Frontiers in Psychology, 7*.
- Conson, M., Aromino, A., & Trojano, L. (2010). Whose hand is this? Handedness and visual perspective modulate self/other discrimination. *Experimental Brain Research, 206*(4), 449-453.
- Conson, M., Mazzarella, E., & Trojano, L. (2011). Self-touch affects motor imagery: a study on posture interference effect. *Experimental Brain Research, 215*(2), 115-122.
- Conson, M., Mazzarella, E., Donnarumma, C., & Trojano, L. (2012). Judging hand laterality from my or your point of view: Interactions between motor imagery and visual perspective. *Neuroscience Letters, 530*(1), 35-40.
- Craver-Lemley, C., & Reeves, A. (1992). How visual imagery interferes with vision. *Psychological Review, 4*(4), 633.
- Cruikshank, L. C., Singhal, A., Hueppelsheuser, M., & Caplan, J. B. (2012). Theta oscillations reflect a putative neural mechanism for human sensorimotor integration. *Journal of Neurophysiology, 107*(1), 65-77.
- Electrical Geodesics, Inc. (2006). NetStation Waveform Tools Technical Manual (Tech. Rep. S-MAN-200-WTFR-001). Eugene, OR: EGI.

- Engelhard, I. M., van den Hout, M. A., & Smeets, M. A. M. (2011). Taxing working memory reduces vividness and emotional intensity of images about the Queen's Day tragedy. *Journal of Behavior Therapy and Experimental Psychiatry*, 42(1), 32–37.
- Daszykowski, M., Walczak, B., & Massart, D. (2002). Looking for Natural Patterns in Analytical Data. 2. Tracing Local Density with OPTICS. *Journal of Chemical Information and Computer Sciences*, 42(3), 500-507.
- Davidson, R., & Schwartz, G. (1977). Brain mechanisms subserving self-generated imagery: Electrophysiological specificity and patterning. *Psychophysiology*, 14(6), 598-602.
- Del Gratta, C., Di Matteo, R., De Nicola, A., Ferretti, A., Tartaro, A., Bonomo, L., ... Belardinelli, M. (2001). Sensory image generation: a comparison between different sensory modalities with fMRI. *Neuroimage*, 13(6), 394.
- Dijkstra, N., Bosch, S. E., & van Gerven, M. A. J. (2019). Shared neural mechanisms of visual perception and imagery. *Trends in Cognitive Sciences*, 23(5), 423–434.
- Ebersbach, M., & Krüger, M. (2017). Let's twist again! Embodiment effects in spatial judgments on human figures rotated along a vertical axis. *Journal of Cognitive Psychology*, 29(8), 963–976.
- Eichenbaum, H. (2012). *The cognitive neuroscience of memory: An introduction*. Oxford University Press.
- Epstein, M. (1980). The Relationship of Mental Imagery and Mental Rehearsal to Performance of a Motor Task. *Journal of Sport Psychology*, 2(3), 211-220.

- Farah, M. J., Hammond, K. M., Levine, D. N., & Calvanio, R. (1988). Visual and spatial mental imagery: dissociable systems of representation. *Cognitive Psychology*, (4), 439.
- Fellrath, J., Mottaz, A., Schnider, A., Guggisberg, A. G., & Ptak, R. (2016). Theta-band functional connectivity in the dorsal fronto-parietal network predicts goal-directed attention. *Neuropsychologia*, 92, 20–30.
- Fiehler, K., & Roesker, F. (2010). Plasticity of multisensory dorsal stream functions: Evidence from congenitally blind and sighted adults. *Restorative Neurology And Neuroscience*, 28(2), 193–205.
- Filgueiras, A., Quintas Conde, E. F., & Hall, C. R. (2018). The neural basis of kinesthetic and visual imagery in sports: an ALE meta-analysis. *Brain Imaging and Behavior*, 12(5), 1513–1523.
- Flindall, J., & Gonzalez, C. (2013). On the evolution of handedness: Evidence for feeding biases. *PLoS ONE*, 8(11): e78967.
- Formaggio, E., Storti, S. F., Boscolo Galazzo, I., Gandolfi, M., Geroi, C., Smania, N., ... Manganotti, P. (2015). Time-frequency modulation of ERD and EEG coherence in robot-assisted hand performance. *Brain Topography*, 28(2), 352–363.
- Gallagher, S. (2005). *How the body shapes the mind*. Oxford University Press, Oxford.
- Gentilucci, M., Daprati, E., & Gangitano, M. (1998). Right-handers and left-handers have different representations of their own hand. *Cognitive Brain Research*, 6(3), 185-192.

Geschwind, N. (2011). Disconnexion syndromes in animals and man. *Selected Papers on Language and the Brain*, 105.

Gerardin, E., Sirigu, A., Lehericy, S., Poline, J.B., Gaymard, B., Marsault, C., Agid, Y., & Le Bihan, D. (2000). Partially Overlapping Neural Networks for Real and Imagined Hand Movements. *Cerebral Cortex*, 10(11), 1093-1104.

Gibson, J. J. (1977). The theory of affordances. *Hilldale, USA*, 1(2).

Gibson, J. J. (2014). *The ecological approach to visual perception: classic edition*. Psychology Press.

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.

Grisoni, L., Dreyer, F. R., & Pulvermüller, F. (2016). Somatotopic semantic priming and prediction in the motor system. *Cerebral Cortex*, 26(5), 2353-2366.

Guérard, K., Lagacé, S., & Brodeur, M. (2015). Four types of manipulability ratings and naming latencies for a set of 560 photographs of objects. *Behavior Research Methods*, 47(2), 443-470.

Guillot, A., Moschberger, K., & Collet, C. (2013). Coupling movement with imagery as a new perspective for motor imagery practice. *Behavioral & Brain Functions*, 9(1), 1–8.

Hall, C., & Pongrac, J. (1983). Movement imagery questionnaire. London, Canada: University of Western Ontario.

- Halpern, A. R., Zatorre, R. J., Bouffard, M., & Johnson, J. A. (2004). Behavioral and neural correlates of perceived and imagined musical timbre. *Neuropsychologia*, (9), 1281.
- Hanna-Pladdy, B., Daniels, S. K., Fieselman, M. A., Thompson, K., Vasterling, J. J., Heilman, K. M., & Foundas, A. L. (2001). Praxis lateralization: errors in right and left hemisphere stroke. *Cortex*, 37(2), 219–230.
- Hauk, O., Johnsrude, I., & Pulvermuller, F. (2004). Somatotopic representation of action words in human motor and premotor cortex. *Neuron*, 41, 301-307.
- Heath, M., Westwood, D., Roy, E., & Young, R. (2002). Manual asymmetries in tool-use: Implications for apraxia. *Laterality*, 7(2), 131-143.
- Heilman, K. M., & Rothi, L. J. G. (2003). Apraxia. In K. M. Heilman & E. Valenstein (Eds.), *Clinical neuropsychology*, 215-235.
- Heremans, E., Feys, P., Nieuwboer, A., Vercruyse, S., Vandenberghe, W., Sharma, N., & Helsen, W. (2011). Motor Imagery Ability in Patients With Early- and Mid-Stage Parkinson Disease. *Neurorehabilitation And Neural Repair*, 25(2), 168–177.
- Hétu, S., Gregoire, M., Saimpont, A., Coll, M.P., Eugene, F., Michon, P.E., & Jackson, P. L. (2013). The neural network of motor imagery: An ALE meta-analysis. *Neuroscience and Biobehavioral Reviews*, (5), 930.
- Hishitani, S. (2009). Auditory imagery questionnaire: Its factorial structure, reliability, and validity. *Journal of Mental Imagery*, 33, 63–80.

- Hoover, A., & Harris, L. (2012). Detecting delay in visual feedback of an action as a monitor of self-recognition. *Experimental Brain Research*, 222(4), 389-397.
- Hoover, A., & Harris, L. (2015). The role of the viewpoint on body ownership. *Experimental Brain Research*, 233(4), 1053-1060.
- Huth, A., de Heer, W., Griffiths, T., Theunissen, F., & Gallant, J. (2016). Natural speech reveals the semantic maps that tile human cerebral cortex. *Nature*, 532(7600), 453-458.
- Igasaki, T., Takemoto, J., & Sakamoto, K. (2018). Relationship between kinesthetic/visual motor imagery difficulty and event-related desynchronization/synchronization. *IEEE Engineering in Medicine and Biology Society*, 1911-1914.
- Ionta, S., & Blanke, O. (2009). Differential influence of hands posture on mental rotation of hands and feet in left and right handers. *Experimental Brain Research*, 195(2), 207-217.
- Ishibashi, R., Mima, T., Fukuyama, H., & Pobric, G. (2018). Facilitation of function and manipulation knowledge of tools using transcranial direct current stimulation (tDCS). *Frontiers in Integrative Neuroscience*, 11(37), 1-8.
- Jäncke, L., Shah, N. J., and Peters, M. (2000). Cortical activations in primary and secondary motor areas for complex bimanual movements in professional pianists. *Cogn. Brain Res.* 10, 177–183

- Järveläinen, J., Schürmann, M., & Hari, R. (2004). Activation of the human primary motor cortex during observation of tool use. *Neuroimage*, *23*(1), 187-192.
- Jeannerod, M. (1994). The representing brain: Neural correlates of motor intention and imagery. *Behavioral And Brain Sciences*, *17*(02), 187.
- Jensen, O., & Tesche, C. D. (2002). Frontal theta activity in humans increases with memory load in a working memory task. *European Journal of Neuroscience*, *15*(8), 1395–1399.
- Jongsma, M. L. A., Meulenbroek, R. G. J., Okely, J., Baas, C. M., van der Lubbe, R. H. J., & Steenbergen, B. (2013). Effects of hand orientation on motor imagery-event related potentials suggest kinesthetic motor imagery to solve the hand laterality judgment task. *Plos One*, *8*(9), e76515.
- Just, M., Cherkassky, V., Aryal, S., & Mitchell, T. (2010). A neurosemantic theory of concrete noun representation based on the underlying brain codes. *PLoS ONE*, *5*(1), e8622.
- Kaminsky, I., & Veraksa, A. (2017). Conventional theories and modern views on the nature of the mental motor image used in sport. *Nacional'nyj Psihologičeskij Žurnal*, *(26)*, 16.
- Kamleitner, B. (2011). When Imagery Influences Spending Decisions: The Role of Ownership Simulations. *Zeitschrift Für Psychologie (2007. Print)*, *(4)*, 231.
- Kaufmann, G. (1981). What is wrong with imagery questionnaires? *Scandinavian Journal of Psychology*, *22*(1), 59-64.

Knecht, S., Drager, B., Deppe, M., Bobe, L., Lohmann, H., Floel, A., Ringelstein, E., & Henningsen, H. (2000). Handedness and hemispheric language dominance in healthy humans. *Brain*, *123*(12), 2512-2518.

Kondo, T., Saeki, M., Hayashi, Y., Nakayashiki, K., & Takata, Y. (2015). Effect of instructive visual stimuli on neurofeedback training for motor imagery-based brain-computer interface. *Human Movement Science*, *43*, 239–249.

Kosslyn, S.M., Brunn, J., Cave, K.R., & Wallach R.W. (1984). Individual differences in mental imagery ability: A computational analysis. *Cognition*, *18*, 195-243.

Kosslyn, S. M., Ganis, G., & Thompson, W. L. (2006). *The case for mental imagery*. Oxford University Press.

Kosslyn, S.M., Thompson, W.L., Shephard, J.M., Ganis, G., Bell, D., Donovitch, J., Wittenberg, L.A., & Alpert N.M. (2004). Brain rCBF and performance in visual imagery tasks: Common and distinct processes. *European Journal of Cognitive Psychology*, *16*, 696-716.

Kozhevnikov, M., Blazhenkova, O., & Becker, M. (2010). Trade-off in object versus spatial visualization abilities: Restriction in the development of visual-processing resources. *Psychonomic Bulletin & Review*, *17*, 29–35.

Kozhevnikov, M., Kosslyn, S., & Shepard, J. (2005). Spatial versus object visualizers: A new characterization of visual cognitive style. *Memory & Cognition*, *(4)*, 710.

- Krause, C.M., Sillanmaki, L., Koivisto, M., Saarela, C., Haggqvist, A., Laine, M., Hamalainen, H., 2000. The effects of memory load on event-related EEGdesynchronization and synchronization. *Clin. Neurophysiol.* 111, 2071–2078.
- Lambert, K., Chen, Y., Madan, C., & Singhal, A. (in prep). The neural correlates of movement imagery: mu rhythm reflects imagery success and ability.
- Lebon, F., Horn, U., Domin, M., & Lotze, M. (2018). Motor imagery training: Kinesthetic imagery strategy and inferior parietal fMRI activation. *Human Brain Mapping*, 39(4), 1805–1813.
- Lenartowicz, A., Lu, S., Rodriguez, C., Lau, E. P., Walshaw, P. D., McCracken, J. T., ... Loo, S. K. (2016). Alpha desynchronization and frontoparietal connectivity during spatial working memory encoding deficits in ADHD: A simultaneous EEGfMRI study. *NeuroImage: Clinical*, 11, 210–223.
- Likert, R., & Quasha, W. (1937). The revised Minnesota paper form board test. *Journal of Educational Psychology*, (3), 197.
- Lindstrom, M.J., & Bates, D.M. (1988). Newton-Raphson and EM algorithms for linear mixed-effects models for repeated-measures data. *Journal of the American Statistical Association*, 83, 1014–1022.
- Liu, R., Wang, Y., Newman, G. I., Thakor, N. V., & Ying, S. (2017). EEG classification with a sequential decision-making method in motor imagery BCI. *International Journal of Neural Systems*, 27(8), 1.
- Llanos, C., Rodriguez, M., Rodriguez-Sabate, C., Morales, I., & Sabate, M. (2013). Mu-rhythm changes during the planning of motor and motor imagery actions. *Neuropsychologia*, (6), 1019.

- Logie, R.H., Pernet, C.R., Buonocore, A., & Della Sala, S. (2011) Low and high imagers activate networks differentially in mental rotation. *Neuropsychologia*, *49*, 3071–3077.
- Lotze, M., Montoya, P., Erb, M., Hülsmann, E., Flor, H., Klose, U., ... Grodd, W. (1999). Activation of cortical and cerebellar motor areas during executed and imagined hand movements: an fMRI study. *Journal Of Cognitive Neuroscience*, *11*(5), 491–501.
- Lotze, M., Scheler, G., Tan, H. R., Braun, C., and Birbaumer, N. (2003). The musician's brain: functional imaging of amateurs and professionals during performance and imagery. *Neuroimage* *20*, 1817–1829.
- Madan, C.R., & Singhal, A. (2012). Motor imagery and higher-level cognition: Four hurdles before research can sprint forward. *Cognitive Processing*, *13*(3), 211-229.
- Madan, C.R., & Singhal, A. (2013). Introducing TAMI: An objective test of ability in movement imagery. *Journal of Motor Behavior*, *45*(2), 153-166.
- Madan, C.R., & Singhal, A. (2014). Improving the TAMI for use with athletes. *Journal of Sports Sciences*, *32*(14), 1351-1356.
- Madan, C. & Singhal, A. (2015). No sex differences in the TAMI. *Cognitive Processing*, *16*(2), 203-209.
- Madan, C., Chen, Y., & Singhal, A. (2016). ERPs differentially reflect automatic and deliberate processing of the functional manipulability of objects. *Frontiers In Human Neuroscience*, *10*, 360.

- Martin, S., Mikutta, C., Leonard, M. K., Hungate, D., Koelsch, S., Shamma, S., ... Pasley, B. N. (2018). Neural Encoding of Auditory Features during Music Perception and Imagery. *Cerebral Cortex*, 28(12), 4222–4233.
- Marzoli, D., Mitaritonna, A., Moretto, F., Carluccio, P., & Tommasi, L. (2011). The handedness of imagined bodies in action and the role of perspective taking. *Brain And Cognition*, 75(1), 51-59.
- Marzoli, D., Palumbo, R., Di Domenico, A., Penolazzi, B., Garganese, P., & Tommasi, L. (2011). The Relation between Self-Reported Empathy and Motor Identification with Imagined Agents. *PLoS ONE*, 6(1), e14595.
- Marzoli, D., Menditto, S., Lucafò, C., & Tommasi, L. (2013). Imagining others' handedness: visual and motor processes in the attribution of the dominant hand to an imagined agent. *Experimental Brain Research*, 229(1), 37-46.
- Marzoli, D., Lucafò, C., Rescigno, C., Mussini, E., Padulo, C., & Prete, G. et al. (2017). Sex-specific effects of posture on the attribution of handedness to an imagined agent. *Experimental Brain Research*, 235(4), 1163-1171.
- McAvinue, L. P., & Robertson, I. H. (2006). Measuring Visual Imagery Ability: A Review. *Imagination, Cognition and Personality*, 26(3), 191–211.
- McKelvie, S. J. (1995). The VVIQ as a psychometric test of individual differences in visual imagery vividness: a critical quantitative review and plea for direction. *Journal of Mental Imagery*, 19, 1–106.

- Mills, K., Gibb, R., MacLean, J., Netelenbos, N., & Gonzalez, C. (2015). The relationship between motor lateralization and executive function. *International Journal Of Developmental Neuroscience*, *47*, 89.
- Mollo, G., Pulvermüller, F., & Hauk, O. (2016). Movement priming of EEG/MEG brain responses for action-words characterizes the link between language and action. *Cortex*, *74*, 262–276.
- Moran, A., Bramham, J., Collet, C., Guillot, A., & MacIntyre, T. (2015). Motor imagery in clinical disorders: importance and implications. *Frontiers in Psychiatry*, *6*, 1-4.
- Moscovitch, D. A., Chiupka, C. A., & Gavric, D. L. (2013). Within the mind's eye: Negative mental imagery activates different emotion regulation strategies in high versus low socially anxious individuals. *Journal of Behavior Therapy & Experimental Psychiatry*, *44*(4), 426–432.
- Moulton, S., & Kosslyn, S. (2009). Imagining Predictions: Mental Imagery as Mental Emulation. *Philosophical Transactions: Biological Sciences*, *364*(1521), 1273.
- Munte, T. F., Altenmüller, E., and Jancke, L. (2002). The musician's brain as a model of neuroplasticity. *Nature Reviews Neuroscience*, *3*, 473–478.
- Munzert, J., Zentgraf, K., Stark, R., & Vaitl, D. (2008). Neural activation in cognitive motor processes: comparing motor imagery and observation of gymnastic movements. *Experimental Brain Research*, *188*(3), 437-444.

- Murphy, S. E., O'Donoghue, M. C., Blackwell, S. E., Nobre, A. C., Browning, M., & Holmes, E. A. (2017). Increased rostral anterior cingulate activity following positive mental imagery training in healthy older adults. *Social Cognitive & Affective Neuroscience*, *12*(12), 1950–1958.
- Muthukumaraswamy, S., Johnson, B., & McNair, N. (2004). Mu rhythm modulation during observation of an object-directed grasp. *Cognitive Brain Research*, *19*(2), 195-201.
- Nam, C. S., Jeon, Y., Kim, Y.J., Lee, I., & Park, K. (2011). Movement imagery-related lateralization of event-related (de)synchronization (ERD/ERS): Motor-imagery duration effects. *Clinical Neurophysiology*, *(3)*, 567.
- Ní Choisdealbha, Á., Brady, N., & Maguinness, C. (2011). Differing roles for the dominant and non-dominant hands in the hand laterality task. *Experimental Brain Research*, *211*(1), 73-85.
- Nico, D., Daprati, E., Rigal, F., Parsons, L., & Sirigu, A. (2004). Left and right hand recognition in upper limb amputees. *Brain*, *127*(1), 120-132.
- Nicola, C., Francesca, B., Stefano F., C., Daniela, P., Andrea, F., Giovanni, B., ... Tim, S. (2008). The Different Neural Correlates of Action and Functional Knowledge in Semantic Memory: An fMRI Study. *Cerebral Cortex*, *(4)*, 740.
- O'Craven, K. M., & Kanwisher, N. (2000). Mental imagery of faces and places activates corresponding stimulus-specific brain regions. *Journal Of Cognitive Neuroscience*, *12*(6), 1013–1023.
- Ochipa, C., Rapcsak, S., Maher, L., Rothi, L., Bowers, D., & Heilman, K. (1997). Selective deficit of praxis imagery in ideomotor apraxia. *Neurology*, 474-480.

Oldfield, R. (1971). The assessment and analysis of handedness: The Edinburgh inventory.

Neuropsychologia, 9(1), 97-113.

Olivetti Belardinelli, M., Di Matteo, R., Del Gratta, C., De Nicola, A., Ferretti, A., Tartaro, A., ... & Luca

Romani, G. (2004). Intermodal sensory image generation: An fMRI analysis. *European Journal of Cognitive Psychology*, 16(5), 729-752.

Onton, J., Delorme, A., & Makeig, S. (2005). Frontal midline EEG dynamics during working memory.

Neuroimage, 27(2), 341–356.

Orr, E. L., Lacourse, M. G., Cohen, M. J., & Cramer, S. C. (2008). Cortical activation during executed,

imagined, and observed foot movements. *Neuroreport*, 19(6), 625-630.

Palermo, L., Iaria, G., & Guariglia, C. (2008). Mental imagery skills and topographical orientation in

humans : A correlation study. *Behavioural Brain Research*, (2), 248.

Palmiero, M., Olivetti Belardinelli, M., Nardo, D., Di Matteo, R., D'Ausilio, A., Sestieri, C., & Romani,

G. L. (2009). Mental imagery generation in different modalities activates sensory-motor areas.

Cognitive Processing, 10(2), 268–271.

Pearl, J., & Mackenzie, D. (2018). *The book of why : the new science of cause and effect*. Basic Books.

Pfurtscheller, G., & Neuper, C. (1997). Motor imagery activates primary sensorimotor area in humans.

Neuroscience Letters, (2–3), 65.

- Pfurtscheller, G., Brunner, C., Schlögl, A., & Lopes da Silva, F. H. (2006). Mu rhythm (de)synchronization and EEG single-trial classification of different motor imagery tasks. *Neuroimage*, *31*(1), 153–159.
- 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*(10), e0198051.
- Pinker, S., & Kosslyn, S. M. (1978). The representation and manipulation of three-dimensional space in mental images. *Journal of Mental Imagery*, *2*(1), 69-84.
- Porro, C., Francescato, M., Cettolo, V., Baraldi, P., & Diamond, M. (1996). Primary motor cortex activity during motor performance and motor imagery: A fMRI study. *Neuroimage*, *3*(3), S214.
- Proskovec, A. L., Wiesman, A. I., Heinrichs-Graham, E., & Wilson, T. W. (2018). Beta Oscillatory Dynamics in the Prefrontal and Superior Temporal Cortices Predict Spatial Working Memory Performance. *Scientific Reports*, *8*(1), 8488.
- Pruitt, T. A., Halpern, A. R., & Pfordresher, P. Q. (2019). Covert singing in anticipatory auditory imagery. *Psychophysiology*, *56*(3), e13297.
- Psychology Software Tools, Inc. [E-Prime 2.0]. (2012). Retrieved from <https://www.pstnet.com>.
- Ptak, R., Schnider, A., & Fellrath, J. (2017). The Dorsal Frontoparietal Network: A core system for emulated action. *Trends in Cognitive Sciences*, *21*(8), 589–599.

Pujol, J., Deus, J., Losilla, J.M., & Capdevila, A. (1999). Cerebral lateralization of language in normal left-handed people studied by functional MRI. *Neurology*, 52, 1038–43.

Pylyshyn, Z. W. (2002). Mental imagery: In search of a theory. *Behavioral and Brain Sciences*, 25(2), 157-182.

Roberts, R., Callow, N., Hardy, L., Markland, D., & Bringer, J. (2008). Movement imagery ability: Development and assessment of a revised version of the Vividness of Movement Imagery Questionnaire. *Journal of Sport & Exercise Psychology*, 30, 200-221.

Roth, M., Decety, J., Raybaudi, M., Massarelli, R., Delon-Martin, C., & Segebarth, C. (1996). Possible involvement of primary motor cortex in mentally simulated movement. *Neuroreport*, 7(7), 1280-1284.

Rinck, M., & Denis, M. (2004). The Metrics of Spatial Distance Traversed During Mental Imagery. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 30(6), 1211-1218.

Rueschemeyer, S., van Rooij, D., Lindemann, O., Willems, R., & Bekkering, H. (2010). The function of words: Distinct neural correlates for words denoting differently manipulable objects. *Journal Of Cognitive Neuroscience*, 22(8), 1844-1851.

Ruggiero, G., Ruotolo, F., & Iachini, T. (2009). The role of vision in egocentric and allocentric spatial frames of reference. *Cognitive Processing*, 10(S2), 283-285.

- Ruthsatz, V., Neuburger, S., Jansen, P., & Quaiser-Pohl, C. (2015). Cars or dolls? Influence of the stereotyped nature of the items on children's mental-rotation performance. *Learning and Individual Differences, 43*, 75-82.
- Sabaté, M., González, B., & Rodríguez, M. (2004). Brain lateralization of motor imagery: motor planning asymmetry as a cause of movement lateralization. *Neuropsychologia, 42*(8), 1041-1049.
- Saccuman, M., Cappa, S., Bates, E., Arevalo, A., Della Rosa, P., Danna, M., & Perani, D. (2006). The impact of semantic reference on word class: An fMRI study of action and object naming. *Neuroimage, 32*(4), 1865-1878.
- Sack, A. T., Jacobs, C., De Martino, F., Staeren, N., Goebel, R., & Formisano, E. (2008). Dynamic premotor-to-parietal interactions during spatial imagery. *Journal of Neuroscience, 28*(34), 8417–8429.
- Scharoun, S. M., & Bryden, P. J. (2014). Hand preference, performance abilities, and hand selection in children. *Frontiers In Psychology, 5*, 82.
- Scheeringa, R., Petersson, K. M., Oostenveld, R., Norris, D. G., Hagoort, P., & Bastiaansen, M. C. M. (2009). Trial-by-trial coupling between EEG and BOLD identifies networks related to alpha and theta EEG power increases during working memory maintenance. *Neuroimage, 44*(3), 1224–1238.
- Schulz, L., Ischebeck, A., Wriessnegger, S. C., Steyrl, D., & Mueller-Putz, G. R. (2018). Action affordances and visuo-spatial complexity in motor imagery: An fMRI study. *Brain and Cognition, 124*, 37–46.

Shweta, C., & Deepak, M. (2015). The use of mental imagery and concentration in the elimination of anxiety and building of self confidence of female cricket players participating at national level. *International Journal of Sports Sciences & Fitness*, 5(1), 86–94.

Schwitzgebel, E. (2002). How well do we know our own conscious experience? The case of visual imagery. *Journal of Consciousness Studies*, 9(5–6), 35–53.

Shou, G., & Ding, L. (2013). Frontal theta EEG dynamics in a real-world air traffic control task. *Conference Proceedings: ... Annual International Conference Of The IEEE Engineering In Medicine And Biology Society. IEEE Engineering In Medicine And Biology Society. Annual Conference*, 5594–5597.

Sirigu, A., and Duhamel, J. (2001). Motor and visual imagery as two complementary but neurally dissociable mental processes. *Journal of Cognitive Neuroscience*, 13(7), 910-919.

Shepard, R. N., & Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science*, 171, 701–703.

Taube, W., Mouthon, M., Leukel, C., Hoogewoud, H. M., Annoni, J. M., & Keller, M. (2015). Brain activity during observation and motor imagery of different balance tasks: an fMRI study. *Cortex*, 64, 102-114.

Thompson, W., Slotnick, S., Burrage, M., & Kosslyn, S. (2009). Two forms of spatial imagery: Neuroimaging evidence. *Psychological Science*, 20(10), 1245.

- Toriyama, H., Ushiba, J., & Ushiyama, J. (2018). Subjective vividness of kinesthetic motor imagery is associated with the similarity in magnitude of sensorimotor event-related desynchronization between motor execution and motor imagery. *Frontiers in human neuroscience*, *12*, 295.
- Valadez, E. A., & Simons, R. F. (2018). The power of frontal midline theta and post-error slowing to predict performance recovery: Evidence for compensatory mechanisms. *Psychophysiology*, *55*(4).
- Wheaton, L. A., Nolte, G., Bohlhalter, S., Fridman, E., & Hallett, M. (2005). Synchronization of parietal and premotor areas during preparation and execution of praxis hand movements. *Clinical Neurophysiology*, *(6)*, 1382.
- Willems, R. M., Toni, I., Hagoort, P., & Casasanto, D. (2009). Body-specific motor imagery of hand actions: neural evidence from right- and left-handers. *Frontiers In Human Neuroscience*, *3*, 39.
- Willems, R. M., Labruna, L., D'Esposito, M., Ivry, R., & Casasanto, D. (2011). A functional role for the motor system in language understanding: Evidence from Theta-Burst Transcranial Magnetic Stimulation. *Psychological Science*, *22*, 849 -854.
- Williams, S. E., Cumming, J., & Edwards, M. G. (2011). The functional equivalence between movement imagery, observation, and execution influences imagery ability. *Research Quarterly for Exercise and Sport*, *82*(3), 555-564.
- Wilson, M. (2002). Six views of embodied cognition. *Psychonomic Bulletin & Review*, *(4)*, 625.

- Wilson, V., Dikman, Z., Bird, E., Williams, J., Schwartz, G., Harmison, R., & Shaw-Thornton, L. (2016). EEG Topographic Mapping of Visual and Kinesthetic Imagery in Swimmers. *Applied Psychophysiology & Biofeedback, 41*(1), 121–127.
- Winlove, C., Milton, F., Ranson, J., Fulford, J., MacKisack, M., Macpherson, F., & Zeman, A. (2018). The neural correlates of visual imagery: A co-ordinate-based meta-analysis. *Cortex, 105*, 4-25.
- Wu, J., Duan, H., Tian, X., Wang, P., & Zhang, K. (2012). The effects of visual imagery on face identification: an ERP study. *Frontiers In Human Neuroscience, 6*, 305.
- Yang, J., and Shu, H. (2013). Passive reading and motor imagery about hand actions and tool-use actions: an fMRI study. *Experimental Brain Research, 232*(2), 453-467.
- Zacks, J. M. (2008). Neuroimaging Studies of Mental Rotation: A Meta-analysis and Review. *Journal of Cognitive Neuroscience, 20*(1), 1–19.
- Zaidel, D. W. (2014). Creativity, brain, and art: Biological and neurological considerations. *Frontiers in Human Neuroscience, 8*.