Mu oscillations and motor imagery performance: A reflection of intra-individual success, not inter-individual ability

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Abstract

Mu oscillations (8-13 Hz), recorded over the human motor cortex, have been shown to consistently suppress during both the imagination and performance of movements; however, its functional significance in the imagery process is currently unclear. Here we examined human electroencephalographic (EEG) oscillations in the context of motor imagery performance as measured by imagery success within participants and imagery ability between participants. We recorded continuous EEG activity while participants performed the Test of Ability in Movement Imagery (TAMI), an objective test of motor imagery task. Results demonstrated that mu oscillatory activity significantly decreased during successful as compared to unsuccessful imagery trials. However, the extent of reduction in mu oscillations did not correlate with overall imagery ability as measured by the total TAMI score. These findings provide further support for the involvement of mu oscillations in indexing motor imagery performance and suggest that mu oscillations may reflect important processes related to imagery accuracy, processes likely related to those underlying overt motor production and motor understanding.

Keywords: motor imagery, electroencephalography(EEG), mu rhythm, imagery ability, imagery success

1. Introduction

Motor imagery refers to the mental rehearsal of movement in the absence of overt motor action (Jeannerod 1995; Madan & Singhal, 2012; Munzert et al., 2009; Munzert et al., 2015). Two different sensory modalities are associated with motor imagery: kinaesthetic and visual (Guillot et al., 2008; Munzert et al., 2009; Roberts et al., 2008). Within motor imagery, the kinaesthetic modality involves the imagination of how the motor action feels within one's body, while the visual modality refers to its visualization (Guillot et al., 2008). This visualization can occur from an internal perspective as if observing oneself acting as one's own eyes, or the external perspective, wherein the individual visualizes themselves performing the motor action as if watching themselves on film (Guillot et al., 2008). Neuroimaging research has indicated that these two modalities activate overlapping yet distinct neural networks (Guillot et al., 2009; Jiang et al., 2015). Namely, both activate the supplementary and premotor areas, while the kinaesthetic modality is associated with greater activation in more motor-associated structures, and the visual modality the occipital cortex (Guillot et al., 2009; Jiang et al., 2015).

Electroencephalographic (EEG) research on motor imagery has focused primarily on mu, an 8-14 Hz rhythm recorded over the sensorimotor region of the human scalp. Prior research has reported that mu activity decreases during motor execution and that this typically occurs in the cortical regions contralateral to the performed movement (McFarland et al., 2000; Neuper & Pfurtscheller, 2010). While this decreased activity is widespread within the lower levels (<10 Hz) of the mu frequency band, within the upper levels (>10 Hz) of the band it is localized to the sensorimotor region that represents the body part being moved (Pfurtscheller et al., 2000). This pattern of decreased mu activity also occurs in motor imagery tasks, which is not surprising given that motor execution and imagery share much of the same neural network (Davidson & Schwartz, 1977; Formaggio et al., 2010; McFarland et al., 2000; Pfurtscheller & Neuper, 1997; Pfurtscheller et al., 2006). However, the decreases in mu that accompany motor execution are typically much greater than those accompanying motor imagery (McFarland et al., 2000).

While research suggests that suppression in mu activity is related to motor imagery, the precise relationship between the two remains unclear. One dominant idea is that motor action and motor imagery share the same neural underpinnings, with physical experience with motor actions enhancing their imagination (McFarland et al., 2000; Neuper & Pfurtscheller, 2010). Specifically, these underpinnings may be indexed by mu rhythm, wherein greater decreases in mu activity reflect greater familiarity with the motor movements (Cannon et al., 2014). For example, ter Horst et al. (2013) explored the process by which mu might facilitate motor imagery through a mental hand-rotation task. During the task, participants were instructed to imagine rotating their hands both medially and laterally to match the shown example hand. They found decreases in mu activity occurred in both the medial and lateral rotation tasks, with this decrease being particularly intense in the medial condition. ter Horst et al. (2013) speculated that this difference in mu activity between medial and lateral rotations was due to participants' familiarity with medial hand rotation. Since medial rotation is more commonly performed in real life, participants may have a stronger motor framework to draw upon during the imagery process, making the rotation easier to imagine (Conson et al., 2020; Ní Choisdealbha et al., 2011).

Additionally, the mu rhythm may act as a marker for motor imagery success, with greater decreases indicative of better imagery performance and more motor experience (Cannon et al., 2014). Wriessnegger et al. (2018) examined whether physical practices could enhance motor imagery. They found that subjects who performed a short physical activity before the motor imagery task had larger mu suppression during motor imagery of the practiced activity as compared to subjects who did not physically perform the activity. Presumably, this physical practice of an imagined movement makes the movement more familiar to an individual. This movement familiarity may then lead to greater decreases in the mu rhythm during the movement's imagination (Daeglau et al., 2020; Wriessnegger et al., 2018). However, others have suggested movement familiarity has little or no effects on mu activity levels in motor imagery. For example, Gibson et al. (2014) asked experienced pianists and ice hockey players to imagine making a slap shot, playing a musical piece on the piano, and squeezing their right hand into a fist. They found that mu activity did not differ based on participant familiarity with imagined actions; in other words, mu activity was similar when pianists imagined playing piano as compared to making a slap shot. Similarly, Di Nota et al. (2017) examined mu activity while groups of ballet dancers, non-ballet dancers, and non-dancers imagined dance-related movements and reported no differences in mu activity between groups. Furthermore, according to the neural efficiency hypothesis, higher-performing individuals may display lower brain activation when performing cognitive tasks (see Neubauer and Fink, 2009, for a review). Using simultaneous EEG-fMRI recording, Yin et al. (2016) reported a negative correlation between mu power and BOLD signals from areas of the sensorimotor network, suggesting a relationship between engagement of the sensorimotor network and a decrease in mu power. Therefore, the neural efficiency hypothesis would predict lower sensorimotor network engagement for a good, experienced motor imager, and thus lesser decreases in mu activity.

In addition to movement familiarity, participants' imagery vividness may also be reflected in mu activity patterns. Self-reported levels of imagery vividness have been widely used as an indicator of motor imagery performance, with more vivid imagers considered to be of higher motor imagery ability (McAvinue & Robertson, 2008). In an interesting study, Toriyama et al. (2018) explored the relationship between imagery vividness and mu activity. They first assessed individual motor imagery ability using the subjective Kinesthetic and Visual Imagery Questionnaire. Mu activity was then measured when subjects performed and imagined motor movements, with differences in mu activity between motor execution and motor imagery found to be significantly less pronounced in individuals who reported higher vividness levels. This suggests that the more vividly an individual imagines a movement, the closer it approximates their neural representation of motor execution. However, no overall differences have been reported in overall mu activity between individuals who report overall high levels of vividness and those who do not (Vasilyev et al., 2017; Toriyama et al., 2018). Comparisons between individuals are likely limited by overall variability in neural rhythms in the population, with baseline mu levels shown to differ significantly between individuals (Blankertz et al., 2010; Tangwiriyasakul et al., 2013; Wriessnegger et al., 2020).

Aside from mu, the alpha rhythm has also been investigated within the context of motor imagery. While it oscillates within the same 8-14 Hz frequency band as mu, alpha is concentrated over the parietal occipital region and has been extensively studied since its discovery over one hundred years ago. The alpha rhythm is implicated in various cognitive functions such as attention (see Klimesch 2012 for a review), long-term memory encoding and retrieval (see Klimesch 1999, Klimesch et al., 2007 for reviews), working memory (Fukuda et al., 2015; Jensen et al., 2002; Klimesch et al., 1999; Miller et al., 2018; Wianda and Ross, 2019), and relaxation/meditation (see Lee et al., 2018 for a review). Most notably, alpha rhythm has been linked to many visual-related processes such as visual encoding, visual processing, visual perception, visual attention, and visual imagery (see Başar, 2012 for a review). While suppression of alpha has been reported in motor imagery tasks, how it relates to motor imagery performance has not been well explored (Brinkman et al., 2014).

Given their similar frequency range, many studies have used the terminology of alpha and mu interchangeably. For example, Di Nota et al. (2017) examined brain activity from both central motor and occipital regions, and referred to the 8 – 14 Hz rhythm recorded over each region as ‘alpha’. In contrast, others have argued that these two rhythms are functionally distinct. ter Horst et al. (2013) referred to the 8-14 Hz activity recorded over the central motor region as mu and that recorded over the occipital region as alpha. The differences in mu activity between medial and lateral rotation imagery were not found in the alpha rhythm, leading the authors to propose that the mu rhythm reflects motor-specific processes and alpha more general attention-related processes. Indeed, the alpha rhythm has been suggested to reflect both inward and outward attention, with decreases in alpha shown to predict visual discrimination performance (Hanslmayr et al., 2005; Hanslmayr et al., 2007; Klimesch, 2012; Mathewson et al., 2009; Romei et al., 2010). As the performance of motor imagery is thought to require inward attention, this required attention may be reflected by decreased alpha activity (Decety, 1996).

Beyond attention, there are other processes alpha may reflect during motor imagery. First, the alpha rhythm has been suggested to function as an ‘inhibition controller’ wherein the activity is decreased when one engages in a cognitive task and activity is increased when one is at rest or disengaged (see Klimesch et al., 2007 for a review). Therefore, motor imagery tasks may engage the sensorimotor regions, an engagement reflected in decreased alpha activity to facilitate a ‘release’ from inhibition in these regions. The alpha rhythm has also been proposed to reflect access and control of what is referred to as “the knowledge system” (Klimesch, 2012). Klimesch (2012) argued that given alpha rhythm’s involvement in various cognitive processes, it may be related to a more domain-general process: the controlling and accessing a knowledge storage system that contains long-term memory, declarative information, or any type of implicit and explicit information. As motor imagery relies on accessing previous motor behaviors (in the case of familiar movements) or general know-how of unfamiliar movements which may be stored in the knowledge system (Madan & Singhal, 2012), the alpha rhythm may facilitate the access of that information.

Further complicating assessment of the neurophysiological mechanisms underlying motor imagery is the wide range of methods used to assess motor imagery performance. Arguably the most common method of assessments is psychometric questionnaires that ask individuals to imagine the performance of particular movements and then rate the vividness of this imagery on a Likert scale (for a review, see McAvinue & Robertson, 2008). As these questionnaires are self-report measures, their results may be confounded by several factors. Individuals may misestimate their ability due to over or under confidence, have differing interpretations of vividness thresholds, or feel pressured to report a certain score (i.e., demand characteristics). To avoid these possible biases, various objective measures have been explored as alternatives for measuring motor imagery ability. For example, in mental chronometry, the time it takes an individual to imagine a movement is compared against that of its physical performance as a means to establish motor imagery accuracy. Another example of an objective assessment is the Test of Ability in Movement Imagery, otherwise known as the TAMI (Madan & Singhal, 2013). In the TAMI, individuals are required to imagine a sequence of basic body movements and then select the body's final positioning from five candidate images. Each question, therefore, has explicit correct and incorrect responses that are not subject to the biases of self-report questionnaires. Correlational investigations suggest that individuals primarily engage the visual modality from an internal perspective when performing the TAMI, although the use of the kinaesthetic modality is not actively discouraged (Madan & Singhal, 2013). The TAMI has been further characterized and compared to a variety of other mental imagery tasks in previous studies (Madan & Singhal, 2015; Madan et al., 2018).

At present, the neurophysiological correlates of motor imagery performance are unclear. Beyond the uncertain roles that both mu and alpha may play in such performance, this lack of clarity is exacerbated by the wide range of assessment measures available and discrepancies between-subject comparisons. In the current study, we employed a large sample of EEG participants (N = 53) to explore the relationship between mu oscillations and their role in motor imagery performance. The motor imagery referred to throughout this study is thus primarily that of the visual modality with an internal perspective. We quantified motor imagery performance in two ways: success and ability, with the former being a within-subjects comparison (i.e., if the subject can successfully imagine a motor behavior) and the latter a between-subjects comparison (i.e., how many motor behaviors a subject can successfully imagine). Therefore, motor imagery success refers to the TAMI trials where the individual provides a correct as opposed to an incorrect response. In contrast, motor imagery ability refers to an individual's overall TAMI score out of ten, which can then be compared against the scores of other individuals.

Specifically, we have two main hypotheses. First, that decreases in the mu rhythm are an indication of sensorimotor network engagement, which indexes motor-imagery success. We, therefore, anticipated mu activity to significantly differ between successful and unsuccessful trials on the TAMI within individuals, with greater suppression occurring in trials with a correct response. Second, we further predicted that decreases in overall mu activity would reflect individual motor-imagery ability. In line with the currently unclear literature, we anticipated two possible, contradictory outcomes. Individuals who score higher on the TAMI may exhibit greater decreases in mu activity as they are better able to engage their sensorimotor network and thus successfully approximate their imagery to performed motor actions. An alternative option reflects the neural efficiency hypothesis, wherein individuals who score *lower* may exhibit greater mu decreases as they require more cortical activation to perform imagery tasks. However, we acknowledge that the documented instability of neural rhythms between individuals could limit such comparisons. Lastly, given the complex connection between the mu and alpha rhythms, we also examined alpha activity as recorded over the occipital region. We anticipated that greater decreases in alpha activity would accompany motor imagery success, given the rhythm's documented association with other cognitive mechanisms that likely facilitate successful motor imagery.

2. Methods

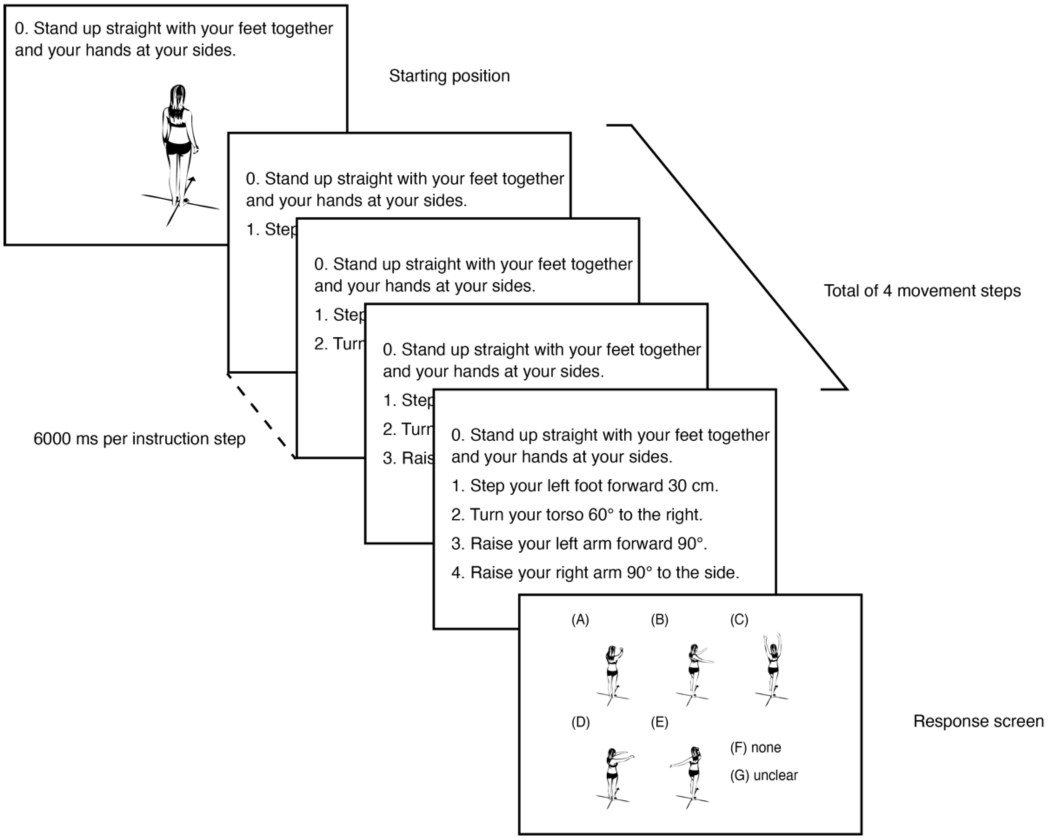
2.1. Participants

A total of 80 introductory psychology students (58 female, 78 right-handers measured by Edinburgh Handedness Inventory; Oldfield, 1971), aged 17 – 34 (M=19.43, SD=2.62) at the University of Alberta participated in the experiment for partial course credit. All participants had normal or corrected-to-normal vision. Written informed consent was obtained prior to the experiment in accordance with the University of Alberta's ethical review board. Data from 23 participants (12 female) were excluded from analysis: 21 due to excessive EEG artifacts, and two due to handedness (score of < 40 on the Edinburgh Handedness Inventory, suggesting ambidextrous or left-handedness). This resulted in a total of 57 students (46 female, 55 right-handers) whose data was fully analyzed.

2.2. Procedure

The experiment was created and run using E-Prime version 2.0 (Psychology Software Tools). Participants completed the Test of Ability in Movement Imagery (TAMI) in an electrically shielded, sound-attenuated chamber. The images and questions were presented in the center of the computer screen on a white background and a practice question preceded the start of the experiment to familiarize participants with the format of the TAMI. Participants were able to proceed with the test upon answering the question correctly. If the participant did not answer the question correctly, they were required to re-attempt the question until arriving at the correct response.

Participants completed 10 questions of the TAMI, with each question made up of four separate movements. Each question begins with the identical instruction, asking the participant to imagine the following starting position: “Stand up straight with your feet together and your hands at your sides”. This instruction was presented alongside an image showing this body position (Starting position, Step 0). The subsequent four steps differed with every question, but each required the individual to imagine the movement of a specific body part. Each step was released after a 6000 ms delay, giving participants time to read the instruction and then imagine the described movement. Once the last step was presented, a response page would appear and present a set of five images showing the possible final body position, along with the choice of “none of the above” and “unclear”. The images remained onscreen until the participants made a response by pressing the number key corresponding to the image of their choice, such as letter key “A” to select body position response “A”. See Figure 1 for a visual breakdown of the procedure.



0. Stand up straight with your feet together and your hands at your sides.
1. Step your left foot forward 30 cm.
2. Turn your torso 60° to the right.
3. Raise your left arm forward 90°.
4. Raise your right arm 90° to the side.

Figure 1. The experimental procedure. Each box illustrated the computer screen at a particular stage in the task (texts and images have been enlarged relative to the screen size to improve the clarity of the figure). Each question starts with an initial standing position followed by four instruction steps. Participants responded by pressing the letter key on the keyboard that corresponds directly to their imagined final body positioning displayed on the screen. There are a total of 10 imagery questions.

2.3. EEG recording and analyses

2.3.1.EEG preprocessing

EEG was recorded using a high-density 256-channel Geodesic Sensor Net (Electrical Geodesics Inc., Eugene, OR), amplified at a gain of 1000, and sampled at 250 Hz. Impedance was kept below 50kΩ and recording was initially referenced to the vertex electrode (Cz). Data was analyzed by custom MATLAB scripts in conjunction with an open-source EEGLAB toolbox (Delorme & Makeig, 2004). The signal was bandpass filtered from 0.1 to 50 Hz and average referenced. Artifacts were corrected via independent component analysis, implemented in EEGLAB. The selection of components was based on visual inspection of the spatial topographies, time courses, and power spectral characteristics of all components (Jung et al., 2000). The components accounting for stereotyped artifacts including eye blinks, eye movements, and muscle movements were removed from the data. Event latencies were corrected with a time lag correction due to a known hardware calibration problem identified by EGI.

2.3.2. Spectra power and duration (Pepisode) analysis

In addition to selecting an objective measure of motor imagery, we also chose an oscillatory quantifying measure that would be relatively selective for rhythmic activity and minimally influenced by non-repeating signals. A method for detecting oscillations, BOSC (Better OSCillation detection; Whitten, et al., 2011; Caplan, et al., 2001) is relatively conservative in its detection of rhythmic activity, with the results more specific to oscillations and less influenced by fleeting increases in power (Chen & Caplan, 2017). This method provides a measure of duration (Pepisode) that indicates the presence of oscillations at the chosen frequency during a specified time window. Using the measure of duration alongside a more conventional power (amplitude) measure of oscillations, therefore, enabled us to better evaluate the functional significance of mu oscillations in motor imagery.

The continuous (unepoched) preprocessed signal was analyzed for oscillatory activity using BOSC. First, the preprocessed EEG signal was convolved with a Morlet wavelet transform with a width of six cycles and sampled at 24 frequencies logarithmically over 1 - 45 Hz range. Power measures were estimated from the square of the instantaneous amplitude of the complex convolution results, and then log-transformed and normalized by dividing the mean log-power from the entire recording session at each frequency band and each electrode. The BOSC method classifies oscillatory events when a segment of signal power at a given frequency exceeds the power threshold for a minimum duration of time (duration threshold). Thus, we set a power and duration threshold to ensure we captured true rhythmic activity. To this end, the power spectrum threshold was calculated to exclude 95% of the signal's background, or colored noise, from the analysis. We set a duration threshold of three cycles to ensure that fleeting increases in power were not considered oscillatory. The result obtained from this method is a duration measure (Pepisode), which represents for a given frequency, the proportion of time rhythmic activity was detected by BOSC. The measure ranges from 0 to 1, where Pepisode = 0.5 means that a given frequency was detected in half of the data.

We focused the analysis on four electrodes, with mu activity examined at C3, C4, and Cz while alpha activity at Oz. The C3, C4, and Cz are the principal electrodes for the motor area. All found over the brain's central region, C3 and C4 are located on opposite sides of the scalp, left and right respectively. Several studies have reported mu oscillations from C3 and C4 during motor imagery tasks (Formaggio et al., 2010; McFarland et al., 2000; Nam et al., 2011; Pfurtscheller & Neuper, 1997; Pfurscheller et al., 2006). Analysis of these electrodes enabled us to make comparisons with findings from similar studies. By also selecting Oz for analysis, a primary electrode for the alpha rhythm, we were able to determine how activity in the mu rhythm differed from other rhythms in the same frequency band.

Our analysis was concentrated on the comparison of activity between unsuccessful and successful trials within the same participant. Given that individuals (N=7) who scored a 10 out of

10 on the TAMI questions had no unsuccessful trials for comparison, their data was excluded from this analysis, reducing the total number of participants to 50. For this approach, mu and alpha frequency bands were defined as 8-14 Hz. Frequencies within each band were collapsed at their respective electrode sites (central electrode sites for the mu rhythm, occipital for alpha) by averaging together the Pepisode values obtained within its previously specified bandwidth. The Pepisode were then averaged together across participants, categorized according to condition (successful vs. unsuccessful trials), and compared using a paired-sample, two-tailed *t*-test.

The primary goal of this study was to investigate if mu oscillations index motor imagery success and ability as measured by an objective imagery assessment tool, the TAMI. We first examined imagery success by contrasting successful and unsuccessful motor imagery trials within a given participant, predicting that less mu oscillations would accompany the successful trials. Next, we investigated individual imagery ability by correlating mu oscillations with performance on the TAMI score across participants. If mu suppression is a reflection of an individual's ability to perform motor imagery, we would expect individuals who score higher on the TAMI to have a greater magnitude of difference in mu oscillatory activity between successful and unsuccessful trials, indicating that their greater motor imagery ability was accompanied by more suppression in the mu rhythm. Alternatively, if mu suppression is a reflection of neural engagement, and high performing individuals are more neurally efficient (per the neural efficiency hypothesis), we would expect individuals who score higher on the TAMI to have a smaller magnitude of difference in mu oscillatory activity between successful and unsuccessful trials, indicating that their greater motor imagery ability was accompanied by less suppression in the mu rhythm.

3. Results

3.1. Behavioral Results

We first analyzed participants' performance on the TAMI as determined by the number of correct trials. The mean score was 7.4 (SD= 1.75) out of 10. This score is comparable to the mean TAMI score reported in Madan & Singhal (2013). Given our sample population was primarily of young, healthy individuals, we also considered the weighting scoring developed by Madan & Singhal (2014). This method helps to reduce the ceiling effect that often accompanies high performance on tasks, by allocating more points based on question difficulty - resulting in between 1 and 5 points per question. The mean weighted score of our participants was 15.6 (s.d. = 5.19) out of 24. Figure 2 illustrates the distribution of participants' TAMI scores, unweighted (A) and weighted (B).

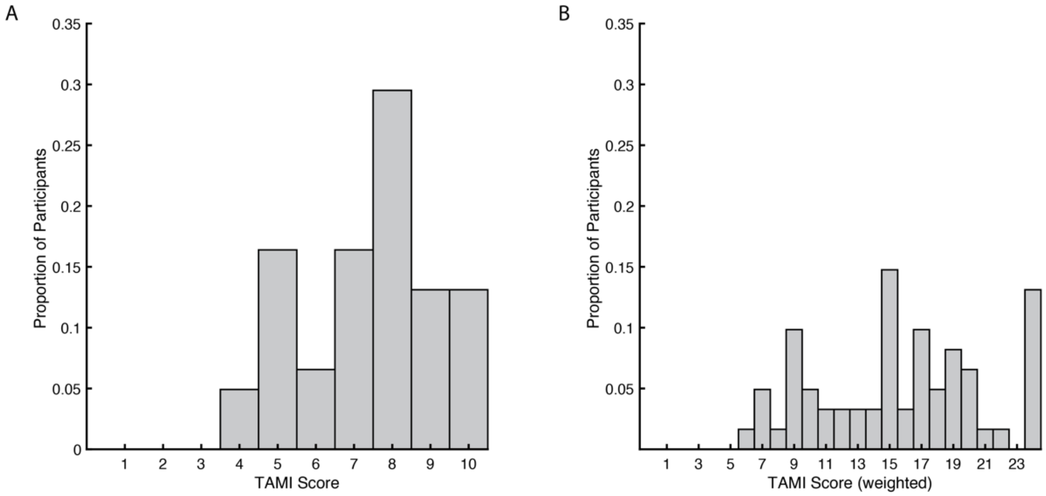


Figure 2. Distribution of participants' scores on the Test of Ability in Movement Imagery (TAMI), A) unweighted, and B) weighted TAMI score.

3.2. Oscillation Results

To test our first hypothesis that suppression in mu activity, as demonstrated by fewer oscillations detected, is associated with successful motor imagery, we compared oscillatory activity between successful and unsuccessful trials within each participant. Trials were scored as "successful" only when participants chose a single correct response to the question. Mu oscillations were quantified using both Power and Pepisodes, a proportional duration measure, at the central electrodes (C3, C4, and Cz). Our time window of analysis was each TAMI question in its entirety, a twenty-four-second "imagery" period that began with the onset of the first movement step and concluded with the offset of the fourth movement step (6000 ms per step). The period during which participants selected their response was not included in this analysis as our focus was on the process, not the end product, of motor imagery. The measures of oscillations (both Pepisode and power) are shown in Figure 3 and summarized in Table 1. Apart from central motor electrodes, we also examined alpha activity over the occipital region (electrodes Oz) due to the rhythm's possible role in motor imagery.

	Pepisodes				Log (power)			
Locations	**Successful**		**Unsuccessful**		**Successful**		**Unsuccessful**	
	M	SD	M	SD	M	SD	M	SD
C3	0.105	0.115	0.126	0.129	0.999	0.065	1.011	0.07
C4	0.111	0.125	0.116	0.123	1.002	0.069	1.009	0.068
Cz	0.105	0.119	0.126	0.133	1.000	0.065	1.010	0.064
Motor	0.107	0.116	0.123	0.123	0.999	0.065	1.008	0.065
Oz (Visual)	0.118	0.122	0.142	0.135	1.007	0.068	1.018	0.067

Table 1. Mean mu activity measured using Pepisode (proportion of oscillatory activity) and Log Power [dB] and their standard deviation (SD) during Successful and unsuccessful trials at different electrode locations.

A repeated-measure ANOVA comparing mu oscillations of imagery success (successful/unsuccessful) × electrode locations (C3/C4/Cz/Oz) revealed a main effect of imagery success as measured by Pepisode, F(1,52) = 18.61, p <.001, due to less presence of mu oscillations during successful trials. A main effect of electrode locations was also significant, F(3,156) = 4.087, p = .008. A Post Hoc pairwise t-test comparison using the Bonferroni correction, with p-value adjusted for comparing a family of 28, revealed no significant effect between central motor electrodes (C3, C4, and Cz), but there were significant differences between the motor electrodes and Oz, the visual electrode (C3 vs. Oz: *t*(52) = -2.692, p(bonf) = .047; C4 vs. Oz: *t*(52) = -3.112, p(bonf)= .013, and Cz vs. Oz: *t*(52) = -2.691, p(bonf)= .047). We, therefore, grouped all central motor electrodes by averaging across the three electrodes for the rest of our analysis. Another repeated-measure ANOVA comparing imagery success (successful/unsuccessful) × electrode locations (motor/visual), revealed a main effect of imagery success as measured by Pepisode, F(1,52) = 15.35, p<.001; and a main effect of electrode location F(1,52) = 11.84, p=.001. The two main effects survived the Post Hoc t-test comparison using Bonferroni correction, with p-value adjusted for comparing a family of 6 (imagery success *t*(52) = -3.918, p(bonf) <.001 and electrode location: *t*(52) = -3.442, p(bonf) = .0001). The interaction of imagery success × electrode locations was not significant (p=.142). Similar results were also found using the same repeated-measure ANOVA examining imagery success measured by wavelet power and electrode locations. There was a main effect of imagery success by power F(1,52) = 12.793, p<.001 and a main effect of location F(1, 52) = 8.431, p = .005. These two main effects survived the Post Hoc t-test comparison using Bonferroni correction (imagery success *t*(52) = -3.577, p(bonf) <.001 and electrode location: *t*(52) = -2.904, p(bonf) = .005). The interaction of imagery success × electrode locations was not significant (p = .587). Together, these results suggest that less mu oscillations were present during motor imagery trials that led to a correct response, indicating mu suppression is associated with successful motor imagery.

In addition, we were interested in how mu oscillations change over time by comparing mu oscillations between successful and unsuccessful trials at each of the four movement steps and the response page at the motor and visual electrodes (Figure 3). A repeated-measures three-way ANOVA comparing imagery success measured by Pepisode (successful/unsuccessful) × Steps (1/2/3/4/Resp/) × electrode locations (motor/visual) revealed a main effect of imagery success, F(1,52) = 7.258, p=.009, a main effect of Steps, F(4,208) = 3.609, p =.007 and a main effect of location, F(1,52) = 12.845, p<.001. There was also a significant imagery success × steps interaction, F(4,208) = 5.023, p<.001 and there was no significant interaction of steps × location (p=.379), imagery success × location (p=.409), and imagery success × steps × location (p=.698). A Post Hoc pairwise t-test comparison using the Bonferroni correction revealed that only the main effects of imagery success (*t*(52) = -2.694, p(bonf)=.009) and locations (*t*(52) = -3.584, p(bonf)<.001) were significant. In addition, only mu oscillations measured at Step 1 significantly differed between successful and unsuccessful trials at the motor (t = -4.306, p(bonf)=.004) and visual (t = -4.887, p(bonf)<.001) electrodes (P-value adjusted for comparing a family of 45). The repeated-measures three-way ANOVA imagery success measured by power (successful/unsuccessful) × Steps (1/2/3/4/Resp/) × electrode locations (motor/visual) revealed similar main effects and interactions (as measured by Pepisode). There is a main effect of imagery success, F(1,52) = 8.383, p = .006, a main effect of Steps, F(4,208) = 6.506, p <.001 and a trending main effect of location F(1,52) = 3.350, p=.073. These results suggest that initial mu suppression at the onset of the motor imagery process is crucial to imagery success and this suppression is less sustained than perhaps previously thought.

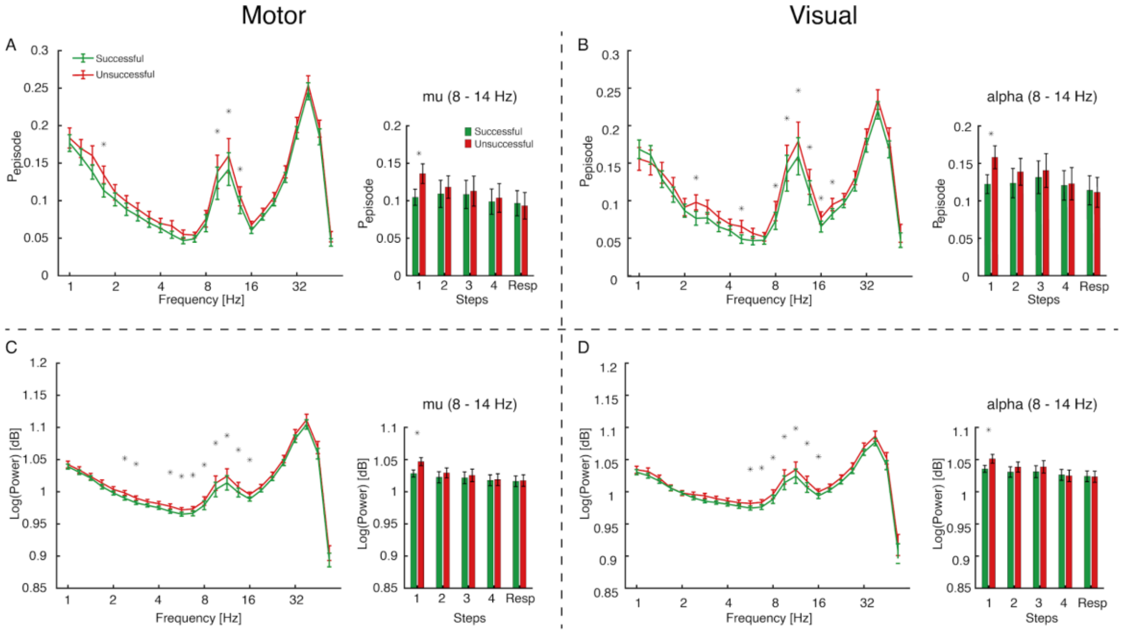


Figure 3. Oscillatory activity and motor-imagery success.

Group average proportion of oscillatory activity (Pepisode) and group average wavelet power (log-transformed) for the entire TAMI question are plotted as a function of frequency between successful (green) and unsuccessful (red) trials. Mu and alpha oscillations are plotted as a function of movement steps (steps 1-4 and response page) between successful (green) and unsuccessful (red) trials. Error bars represent 95% confidence intervals and * denotes a significant pairwise t-test ($p < .05$) difference between successful and unsuccessful imagery trials.

We next tested our second hypothesis: that suppression of mu oscillations may index individual motor imagery ability. We quantified the mu oscillation suppression using the difference measure by calculating the mu oscillation Pepisode difference between successful and unsuccessful trials within individuals. We chose to examine this difference measure of mu oscillations, because the difference measure infers the relationship between one's ability to suppress mu oscillations and motor imagery ability, indicating that a high-motor-imagery-ability individual may possess a greater ability to suppress mu oscillations. To test this possible behavioral-relevance of mu oscillations, we first correlated across participants the difference in mu oscillation suppression (successful - unsuccessful) with TAMI scores (both weighted and unweighted), and scatter plots illustrating the relationship are shown in Figure 4. We found no significant correlation between mu oscillation suppression measured by Pepisode and TAMI scores [unweighted: motor: r(51) = -.093, p =.509; visual r(51) = -.171, p=.220; and weighted: motor: r(51) = -.20, p=.152; visual r(51) = -.187, p=.179]. Since we found suppression of mu oscillations to be strongest at the initial movement step, we also examined the relationship between mu oscillations from step 1 and TAMI scores. We correlated the mu oscillation difference measure (successful-unsuccessful) that occurred during the step 1 time window alone with TAMI scores (both weighted and unweighted). There remained no significant correlation [unweighted: motor: r(51) =- .015, p=.915; visual r(51) = -0.012, p=.930; and weighted: motor: r(51) = .115, p=.413; visual r(51) = .141, p=.314]. We also performed the same correlations using the wavelet power measure, and again found no significant correlations.

These null correlations suggest that the individual differences in mu oscillations, measured by the difference between successful and unsuccessful trials, do not reflect individual motor imagery ability as measured by the TAMI. Apart from the central motor electrodes, when we examined alpha activity over the occipital region (electrodes Oz) using the same analysis approach, we found results similar to those of the mu oscillations recorded from motor electrodes. This suggests that alpha oscillations are also not a reflection of individual motor imagery ability.

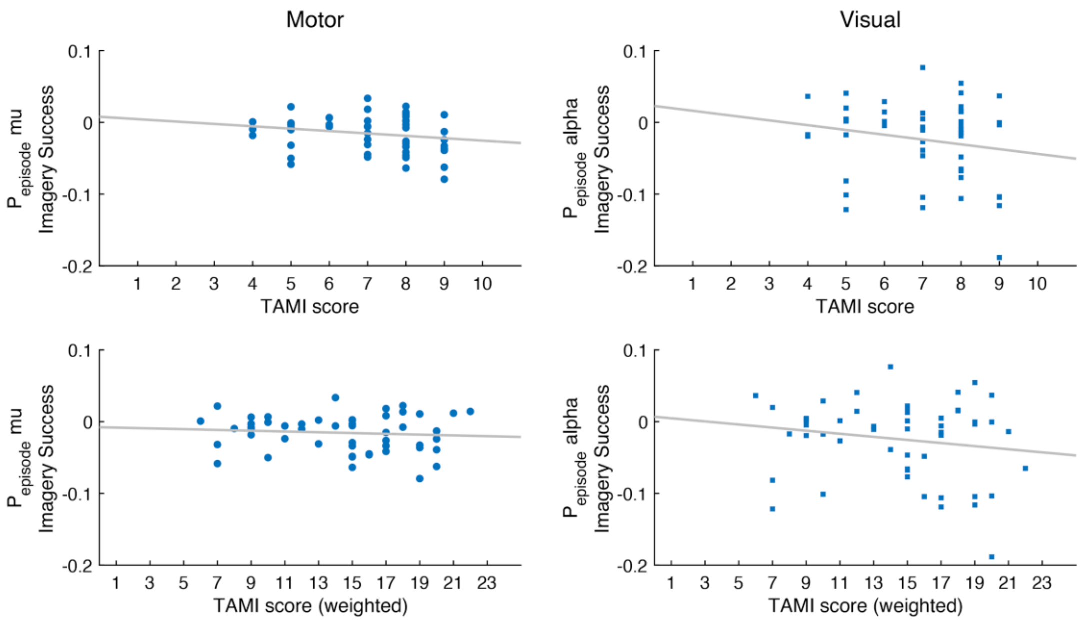


Figure 4. Relationship between the size of motor imagery success (successful - unsuccessful) in the mu and alpha band and TAMI scores (unweighted and weighted). Each point represents single participants. The motor imagery success measure is the proportion of oscillations (Pepisode) for successful minus unsuccessful.

4. Discussion

The current study aimed to examine how mu oscillations vary according to motor imagery performance. We found that successful trials on an objective motor imagery task were accompanied by greater decreases in mu activity as compared to unsuccessful trials. However, this decrease in activity with successful performance within individuals did not correspond to differences in inter-individual motor imagery ability. Individuals who received higher overall scores on the task, both unweighted and weighted, and would therefore be considered to have higher imagery ability, did not exhibit a significantly different motor imagery success effect of mu activity (successful - unsuccessful trials), when compared to those with lower overall scores.

We were able to make confident comparisons between successful and unsuccessful performance due to the objective nature of our measure, with the TAMI requiring participants to make explicitly correct or incorrect responses. A key result, therefore, was the difference found between successful and unsuccessful trials, with less mu oscillations present during imagery that would later generate a correct response. This difference in activity between successful and unsuccessful responses was anticipated based on the findings of previous research (ter Horst et al.., 2013; Ono et al., 2018; Pichiorri et al., 2015). Greater decreases in mu activity have been found to accompany motor imagery of more familiar movements, movements which are likely easier for individuals to picture and thus more successfully imagined (ter Horst et al., 2013). Further, Brain Computer Interface (BCI) research has demonstrated that corrective feedback during imagery, designed to increase the accuracy of the imagery process, leads to reduced mu activity (Ono et al., 2018; Pichiorri et al., 2015). This supports the hypothesis that mu oscillations may reflect motor imagery success within an individual.

Yet it is likely that our results provide only a limited picture of motor imagery success. Guillot et al. (2010) proposed motor imagery performance should be considered in terms of three separate dimensions: vividness, controllability, and exactness. Vividness refers to the sensory richness of the self-generated image, and exactness the imagery's accuracy, while controllability reflects the ease of the image's manipulation (Guillot et al., 2010). In a recent study, Mizuguchi et al. (2019) found that vividness and accuracy of motor imagery were associated with separate neural regions, indicating that patterns of neural activity during a motor imagery task will depend on the dimension being emphasized. As the TAMI emphasizes accurate responses, it likely places more precedence on exactness than self-report vividness questionnaires. Thus, our results may not necessarily be reproduced by a measure that prioritized the vividness dimension.

If successful responses within individuals result in decreased mu activity, it would make intuitive sense that good imagers, who by definition have more successful responses on the TAMI, would have less mu oscillatory activity overall than poor imagers. Alternatively, the neural efficiency hypothesis predicts that good imagers would have a more efficient neural presentation, who would induce less sensorimotor network engagement indexed by less mu activity decrease. However, this was not the case, and our previous results were not echoed in the between-subjects comparison. While both good imagers (TAMI scores > 6) and poor imagers (TAMI scores ≤ 6) exhibited decreases in mu oscillatory activity during successful trials, the good imagers demonstrated no less overall mu activity than their poorer scoring counterparts. This result is in line with other research, wherein individuals with higher scores on the vividness self-report questionnaires did not exhibit greater decreases in mu activity as compared to individuals with lower scores (Toriyama et al., 2018; Vasilyev et al., 2017). The lack of difference in oscillatory activity as a function of overall motor imagery ability may be a result of the mu rhythm's quantitative instability and variability across the populations (Blankertz et al., 2010; Tangwiriyasakul et al., 2013). When taken into consideration with prior findings, our results suggest that overall levels of the mu rhythm should not be used to index overall motor imagery ability between individuals, but rather as a possible measurement of success within an individual's motor imagery performance. This finding may be of particular relevance in terms of motor imagery training protocols. The mu rhythm could be used as a neurophysiological marker to indicate if training has helped an individual to become more successful at motor imagery over time.

Beyond mu oscillations, we also found less alpha activity over the occipital region during successful motor imagery when compared to unsuccessful motor imagery. Alpha oscillations have been linked to a variety of cognitive tasks and are traditionally thought to reflect cortical activation (Klimesch, 1999; Klimesch, 2012). More recently, the alpha rhythm was proposed to reflect inhibition, with decreased alpha activity reflecting a release from inhibition that "sharpens" an individual's attentional view and enables them to better process on task demands (Cooper et al., 2003; Klimesch, et al., 2007; Jensen & Mazaheri, 2010). Moreover, other research has also suggested alpha activity is sensitive to attentional demands. The differences in alpha activity we observed between successful and unsuccessful responses may reflect attentional states, where more alpha activity inhibited the motor imagery process from fully taking place. In addition, alpha oscillations have also been suggested to reflect working memory function, wherein effortful attention is required to hold information in the mind. Indeed, activity in the alpha rhythm has been shown to decrease as working memory load increases (Gevins et al., 1997). Perhaps participants who were successful in holding information in their mind may respond correctly to the TAMI questions.

Further, it is also important to consider the function of alpha oscillations in visual imagery and its contribution to motor imagery. There are two main oppositional findings of alpha oscillations and visual imagery. First, increases in alpha activity are associated with the imagery process. Many prior studies have suggested that alpha oscillations support the maintenance of internal representations and are essential to the successful imagination of a visual object or a sequence of motor movements (see Klimesch et al., 2007 for a review). When Bartsch et al. (2015) asked participants to imagine visual objects based on the verbal instructions given, they found an association between increased alpha power and word-prompted mental imagery. However, decreases in alpha activity are also associated with the imagery process, stemming from the idea that visual perception and visual imagery may rely on similar neural substrates as indexed by alpha suppression (Lee et al., 2012). For example, during a mental rotation task, Michel et al. (1994) found less alpha activity during the process of mental visual imagery. Although the TAMI is a motor imagery task, it encourages the use of the visual modality by asking participants to visualize the described movements. The alpha oscillations measured over the occipital regions may reflect participant engagement of the visual modality during the task. While we may not be able to resolve the debate on alpha activity and motor imagery, we added additional evidence that reduced alpha activity is associated with objective success in motor imagery.

Interestingly, the significant differences in alpha and mu oscillatory activity found between successful and unsuccessful responses occurred only at the first of the four motor imagery steps of the TAMI. The initial step of the TAMI occurs immediately after the presentation of the starting body position and is the first moment wherein the participants are required to manipulate an image in their minds. This result would suggest it is mu activity at the onset of the motor imagery that is essential to successful performance as opposed to its activity throughout the entire imagery process. Perhaps the mu rhythm reflects the generation of the initial motor representation, a possibility supported by its documented suppression during the planning of both imagined and executed motor tasks (Llanos et al., 2013). In an action observation task, Aleksandrov & Tugin (2012) found that suppression in the mu rhythm was greatest at the beginning of the task, with this suppression lessening as it progressed. They proposed that this pattern may stem from less attention being required during a motor-related task once the initial motor preparation stage has been completed (Aleksandrov & Tugin, 2012). Further, the initial decrease in alpha activity may reflect the anticipatory attention wherein a larger decrease in alpha activity was predictive of better visual discrimination performance (Hanslmayr et al., 2005; Hanslmayr et al., 2007; Mathewson et al., 2009; Romei et al., 2010). This anticipatory attention might be important for participants in initializing the motor imagery process.

Our study has added to the literature regarding the neurophysiological correlates of motor imagery performance, indicating that decreases in alpha and mu activity accompany more successful motor imagery performance within an individual. This decrease is particularly significant in the early stages of the imagery process. However, our study is accompanied by some significant limitations. In particular, we recorded neurophysiological activity over a long time window, during which participants were required to both read instructions and imagine the described movements. Thus, the results are not a pure reflection of motor imagery. Not including any comparison conditions limits the conclusions we can draw regarding the mu and alpha rhythm’s respective roles in motor imagery performance. It may be that mu and alpha support motor imagery performance due to involvement in more general underlying cognitive processes. Conditions such as a working memory task, visual attention task, or attentionally demanding non-imagery motor task would have provided valuable insight and are recommended for future investigations. A comparison of differences in scores and neurophysiological activity across measurements of motor imagery ability would also allow for a deeper investigation into the overlap and distinction of its different dimensions. Finally, it cannot confidently be ruled out that inter-individual differences in neural rhythms prevented the detection of correlates between overall mu activity and motor imagery ability.

5. Conclusion

The present study provides evidence that mu oscillations and intra-individual imagery success are related. Our finding of decreased mu activity during successful responses to the TAMI is in line with previous research linking the rhythm to imagery success. However, no significant differences in the rate of occurrence of mu oscillatory activity were found between individuals of high imagery ability and those of lower imagery ability. This suggests that mu oscillations may index successful imagery performance within an individual but cannot be used to make comparisons across a population. Further, results in the occipital region suggest that internal visual imagery, as reflected by the reductions in the alpha rhythm, may facilitate the process of motor imagery in TAMI.

Acknowledgments

The authors would like to thank Vivian Chan and Tristan Pasek for their help in collecting EEG data, and Drs. Ada Leung and Eleonora Bartoli for helpful comments on the manuscript. This research was partly funded by the Natural Sciences and Engineering Research Council of Canada, the Canada Foundation for Innovation, and the University of Alberta Neuroscience and Mental Health Institute.

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