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Handedness effects on imagery of dominant- versus non-dominant-hand movements: An electroencephalographic investigation

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Abstract

Mental representations of our bodies are thought to influence how we interact with our surroundings. We can examine these mental representations through motor imagery, the imagination of movement using scalp EEG recordings. The visual modality of motor imagery emphasises 'seeing' the imagined movement and is associated with increased activity in the alpha rhythm (8–14 Hz) measured over the occipital regions. The kinaesthetic modality emphasises 'feeling' the movement and is associated with decreased activity in the mu rhythm (8–14 Hz) measured over the sensorimotor cortices. These two modalities can be engaged in isolation or together. We recorded EEG activity while 37 participants (17 left-hand dominant) completed an objective hand motor imagery task. Left-handers exhibited significant activity differences between occipital and motor regions only during imagery of right-hand (non-dominant-hand) movements. This difference was primarily driven by less oscillatory activity in the mu rhythm, which may reflect a shift in imagery strategy wherein participants placed more effort into generating the kinaesthetic sensations of non-dominant-hand imagery. Spatial features of 8–14 Hz activity generated from principal component analysis (PCA) provide further support for a strategy shift. Right-handers also exhibited significant differences between alpha and mu activity during imagery of non-dominant movements. However, this difference was not primarily driven by either rhythm, and no differences were observed in the group's PCA results. Together, these findings indicate that individuals imagine movement differently when it involves their dominant versus non-dominant hand, and left-handers may be more flexible in their motor imagery strategies.

Abbreviations: BOSC, better oscillation detection method; EEG, electroencephalography; LH, left-handed; PCA, principal component analysis; RH, right-handed; TAMI, Test of Ability in Movement Imagery; TAMIh, Test of Ability in Movement Imagery–Hand.

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KEYWORDS
alpha rhythm, handedness, motor imagery, mu rhythm

1 | INTRODUCTION

Embodied cognition presumes that all mental processes are shaped by the body and its sensorimotor interactions with the environment (Casasanto, 2009; Garbarini & Adenzato, 2004; Madan & Singhal, 2012; Wilson, 2002). The development of cognition through bodily experience is a foundation for the body-specific hypothesis, which argues that individuals with different bodies engage differently with their surroundings and thus should exhibit different ways of thinking (Casasanto, 2009). As right-handed (RH) individuals and left-handed (LH) individuals use their bodies in systematically different ways, investigating how mental processes vary as a function of hand dominance provides an ideal means to investigate this hypothesis (Brunyé et al., 2012; Conson et al., 2010; Willems et al., 2010). One such mental process is motor imagery or the imagination of action without its physical execution (Madan & Singhal, 2012). Motor imagery primarily involves two sensory modalities: visual and kinaesthetic. The visual modality involves visualisation of the imagined movement, while the kinaesthetic modality requires an individual to imagine the movement's feeling. These two modalities are not mutually exclusive. For example, individuals engage the visual modality even when instructed to use the kinaesthetic during imagery of unfamiliar movements, suggesting that the visual modality is engaged to supplement the unfamiliar movement's less vivid kinaesthetic image (Mizuguchi et al., 2016; Olsson et al., 2008).

Several findings point to a relationship between handedness and motor imagery performance. Individuals are more familiar with using their dominant hand to execute movements (Dirnberger et al., 2011; Ní Choisdealbha et al., 2011). It has been proposed that mental representations of unfamiliar actions are comparatively less well-established than those carried out regularly (Olsson & Nyberg, 2010). Consequently, imagined movements that rely on these representations are more difficult to execute successfully (Olsson & Nyberg, 2010). In keeping with this perspective, RH individuals are significantly more accurate when imagining functional movements involving the right as opposed to left hand (Donoff et al., 2018; Gandrey et al., 2013; Maruff et al., 1999). RH individuals report motor imagery involving the left hand as being less vivid (Matsuo et al., 2020).

Additional evidence can be taken from the hand laterality judgement task, which involves identifying the laterality of hands presented at different angles (Jones et al., 2021). RH individuals are consistently quicker when identifying images of their dominant hand (i.e., right hands), a pattern that does not reliably occur in LH individuals (Conson et al., 2010; Ionta & Blanke, 2009; Jones et al., 2021; Ní Choisdealbha et al., 2011). This decreased laterality effect may result from greater experience of LH individuals using their non-dominant hand (Gonzalez et al., 2007). Further, incongruencies between participant physical body position and target hand position consistently disrupt imagery of the dominant hand only in RH individuals (Conson et al., 2010; Ionta & Blanke, 2009; Jones et al., 2021; Ní Choisdealbha et al., 2011). This group difference may reflect modality preference, with LH individuals primarily engaging the visual modality while RH individuals engaged the kinaesthetic (Ní Choisdealbha et al., 2011).

Neural oscillations measured using electroencephalography (EEG) have been identified as putative neural markers for the visual and kinaesthetic modalities g(Neuper et al., 2005). The visual modality is accompanied by increased activity in the alpha rhythm (8–14 Hz) at the occipital regions of the brain (Bartsch et al., 2015; Chholak et al., 2019; Neuper et al., 2005; Zapała et al., 2021). Alpha is prominently viewed as an inhibitory rhythm, and this increase in the rhythm's activity may reflect the top-down inhibition of external sensory information during tasks that require an internal direction of attention (Bartsch et al., 2015; Cooper et al., 2003; Klimesch et al., 2007). The documented increase in alpha oscillations over occipital regions may therefore reflect inhibited processing of visual stimuli in favour of internally generated mental images (Bartsch et al., 2015; Zapała et al., 2021).

Engagement of the kinaesthetic modality is accompanied by decreased activity in the mu rhythm (8–14 Hz) over the motor regions of the brain (Chen et al., 2021; Neuper et al., 2005). While the mu rhythm oscillates in the same frequency band as the alpha rhythm, mu activity is recorded over sensorimotor as opposed to occipital regions of the brain (Pfurtscheller et al., 2006; Pineda, 2005). Mu activity is negatively correlated with fMRI BOLD activity from areas of the sensorimotor network, suggesting that less mu activity indicates greater involvement of sensorimotor cortices (Yin et al., 2016). Previous research has documented a relationship between mu oscillations and motor imagery performance, in terms of both the accuracy and vividness of the imagined movement (Chen et al., 2021; Toriyama et al., 2018).

Zapała et al. (2020) investigated handedness effects on mu activity and the ability to control a brain–computer interface (BCI). In particular, participants used motor imagery to control the direction of a falling cursor. RH participants achieved greater BCI control than LH participants, with BCI aptitude correlating with mu suppression recorded during an offline version of the same imagery task. LH participants exhibited weaker mu suppression than RH participants, but only at the right motor region during imagery that involved the left-hand. The authors identified two possible contributors to these between-group differences. First, handedness may affect the distribution of the motor control network, with greater lateralisation of activity occurring in RH participants. Second, RH individuals may rely more on the kinaesthetic modality when imagining movements as compared to LH individuals.

A follow up study by Zapała et al. (2021) further examined handedness effects on modality use during motor imagery. Participants were instructed to imagine a sequence of finger tapping movements using either the visual or kinaesthetic modality. Behaviourally, LH participants achieved greater accuracy than RH participants regardless of modality. Engagement of the visual modality was accompanied by an increase in alpha activity over the occipital region only in LH participants. However, topographic maps suggested that RH participants did not change modality as instructed (Zapała et al., 2021). In LH participants, imagery of the right hand using the kinaesthetic modality was accompanied by bilateral mu suppression. One explanation for this result is that LH participants put more effort into generating the comparatively unfamiliar kinaesthetic sensations of the non-dominant hand.

The present study sought to further understand how LH individuals and RH individuals imagine movements with their dominant versus non-dominant hand. We did not emphasise the use of either imagery modality as we sought to understand if individuals implicitly shift strategy according to personal motor experience. Recordings of both alpha and mu activity during the motor imagery task provided respective neural markers of visual and kinaesthetic modalities, and principal component analysis (PCA) was used to further illuminate the spatial distributions of this activity. From the previous literature, we hypothesised that LH participants would perform motor imagery more accurately than RH participants, the latter of whom would be slower and less accurate when imagining movements that involve their non-dominant hand. As individuals generally have less motor experience with their non-dominant hand, we anticipated that imagery involving this hand would be accompanied by increased alpha activity in the occipital region, reflecting a greater emphasis on the visual modality. However, it is also possible that imagery of non-dominant-hand movements leads to greater suppression in the mu rhythm, due to the increased effort needed to generate the 'feel' of the hand's movement.

2 | METHODS

2.1 | Participants

A total of 42 undergraduate students (21 LH; 29 female) with an average age of 19.23 years ($SD = 1.42$) participated to earn credit for an introductory undergraduate psychology course. All participants had normal or corrected-to-normal vision. Written informed consent was obtained before the experiment. Handedness was measured using the Edinburgh Handedness Inventory (EHI), where a Laterality Quotient (LQ) of 50 indicates ambidexterity[26] (M_{RH} [SD] LQ = 87.33 [11.40]; M_{LH} [SD] LQ = 11.29 [14.53], Oldfield, 1971). Data from seven participants were excluded from the analysis: three due to excessive artefacts detected in the EEG, three due to an ambidextrous score on the EHI and one due to outlying performance (>3 standard deviations outside the mean). These exclusions resulted in a final analysis of data from 37 students (17 LH; 24 female).

2.2 | Procedure

Written informed consent was obtained before the experiment, and an institutional ethical review board approved the procedure. Participants completed the Test of Ability in Movement Imagery–Hand (TAMIh), an imagery task of isolated hand movements, in an electrically shielded, sound-attenuated chamber. This task was adapted from Donoff et al. (2018). The experiment was created and run using E-Prime version 2.0 (Psychology Software Tools). The images and questions were presented on a white background in the centre of the computer screen. The task was divided into two separate blocks: (1) left-hand questions and (2) right-hand questions. The order of these two blocks was randomised between participants. Each block contained 10 questions in addition to a practice question intended to familiarise participants with the task's format. For each block, participants held a tennis ball in the hand they were imagining to provide a uniform hand position and reduce the frequency of explicit hand movements. They were not instructed to use a particular sensory modality during imagery. Response input was provided through a keyboard.

Each TAMIh question began with an image of an open hand depicting 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. Participants were instructed to begin imagery at the onset of the first instruction. An example of the five 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 were presented. A command would be displayed for 5000 ms until the following command appeared. Following the display of the fifth command, a response screen would appear and present a set of four images showing the possible final hand position given the preceding sequence of imagined movements, along with the choice of 'unclear'. These images remained onscreen until the participant pressed the letter key corresponding to their position of choice, such as the letter 'B' for the hand position 'B'. The procedure is outlined in Figure 1. We tracked response accuracy and response time as behavioural measures. If the button press selected by the participants matched the target final hand position, we would consider the trial to be 'successful'. Response time was measured by the time latency from onset of response screen to participant's button press. Response time was measured in milliseconds (ms).

2.3 | EEG recording and analysis

2.3.1 | EEG recording

EEG was recorded using a 256-channel high-density array net (Electrical Geodesics Inc., Eugene, OR). The signal was amplified at a gain of 1000 and sampled at 250 Hz, with impedance kept below 50 kΩ. Each recording was initially referenced to the vertex electrode (Cz).

2.3.2 | Data processing and analysis

Data were then analysed using custom MATLAB scripts and the EEGLab open-source toolbox (Delorme & Makeig, 2004). The signal was band-pass filtered using a high-pass filter of 0.1 Hz and then a low-pass filter of 50 Hz. The filtered signal was average re-referenced to a common average. Independent component analysis implemented in EEGLAB was used to identify artefacts in the data (Jung et al., 2000). Artefacts were corrected through independent component analysis. Artefactual components were identified through the visual inspection of each component's spatial topographies, time courses and power spectral characteristics. Components reflecting stereotyped artefacts, such as eye blinks and muscle movement, were removed from the data.

After preprocessing, the continuous EEG recording was analysed for oscillations using the better oscillation detection method (BOSC). This wavelet-based detection method provides a conservative approach to detecting

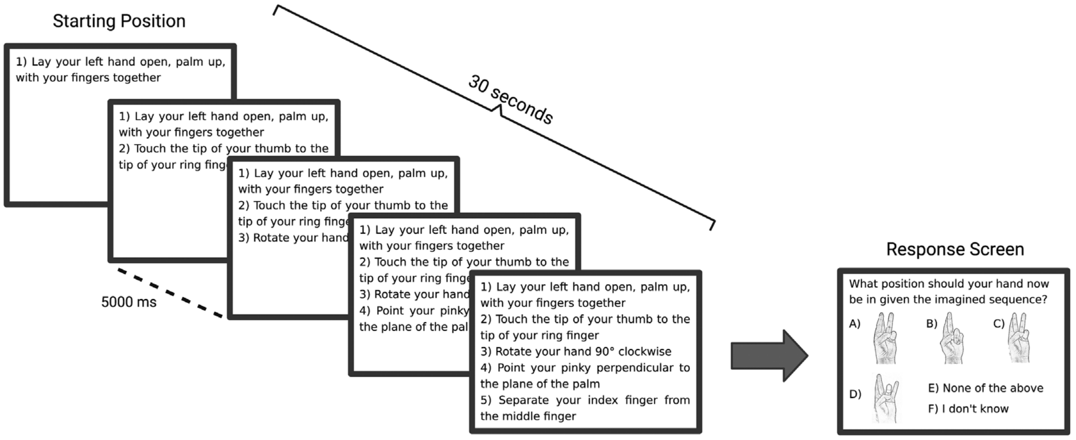

FIGURE 1 The TAMIh procedure. Each box illustrates the computer screen at a particular stage in a task trial (texts and images have been enlarged relative to the screen size to improve the clarity of the figure). Each question began with an initial hand position followed by four commands. Participants were instructed to begin imagery when the description of the initial hand position appeared onscreen. No specific instructions were given to participants regarding which sensory modality to emphasise. Participants responded by pressing the keyboard letter key that corresponds directly to their imagined final hand position displayed on the screen. The task contained a total of 20 questions: 10 for the left hand and 10 for the right hand. The time window of analysis for oscillatory analysis ran from the onset of the initial hand position description to the offset of the final command.

rhythmic activity (Caplan et al., 2001, Whitten et al., 2011). A disadvantage of traditional power analyses is their susceptibility to non-rhythmic signals, as transient artefacts can contribute to sharp changes in a signal's power spectrum. BOSC provides a comparatively conservative approach to oscillation detection. Segments of the signal are only classified as oscillatory when the power at a given frequency exceeds a particular power threshold for a set duration of time, which is described in full detail in Caplan et al. (2001) and Whitten et al. (2011). Here, we briefly outline the major steps taken to implement the BOSC method. (1) Morlet wavelet decomposition: after preprocessing, the entire EEG signal from a given electrode was decomposed using Morlet wavelets with centre frequencies spaced logarithmically from 1 to 50 Hz (6 cycles). (2) Model and estimate the background spectrum: Averaged wavelet power spectrum from the entire experiment was calculated and modelled as coloured noise (i.e., power scaling as 1/frequency) with possible additions of peaks at frequencies that may potentially reflect the presence of oscillations (see examples in Hughes et al., 2011, and Whitten et al., 2011). A linear regression was fit to the power spectrum in log–log space. (3) Oscillation detection: the power threshold for oscillation detection was set to the 95th percentile of the theoretical probability distribution of power values at a given frequency of all signals (background spectrum), and the duration threshold was set at each frequency to three complete cycles. Oscillations were only detected when both power and duration thresholds were exceeded. The resulting measure is the P_{episode}, which reflects the proportion of oscillations at a given frequency detected during a given time period. P_{episode} values range from 0 to 1, with a value of 0.5 indicating that oscillations were detected in half the data. It is important to note that P_{episode} measures duration rather than amplitude and ensures that results are related to sustained rhythmic activity and cannot be explained by other non-repeating signals.

Trials were separated according to condition (left-hand versus right-hand questions), group (LH versus RH) and response (correct versus incorrect) type. The time window of analysis was trimmed to only include data from the onset of Step 1 to the offset of Step 5 at each TAMIh question. Event latencies were corrected with a 36 ms time-lag correction due to a known hardware calibration problem identified by Electrical Geodesics Inc. Data analysis focused on two clusters of electrodes: a Cz-C3-C4 cluster and an Oz-O1-O2 cluster. Cz, C3 and C4 are the principal electrodes for the motor cluster. Cz is located over the brain's midline, while C3 and C4 are, respectively, located over the left and right hemispheres. A decrease in mu oscillations over these three electrodes during motor imagery has been previously reported in the literature (Formaggio et al., 2010). Oz, O1 and O2 are the primary electrodes for the occipital cluster. Oz is located over the occipital midline, while O1 and O2 are, respectively, located over the left and right hemispheres of the occipital region. Alpha oscillations are shown to increase over this area during vision-related tasks, including visual imagery. Including the occipital cluster in our analysis enabled us to examine the possible involvement of visual imagery in the experimental task. The selection of 8–14 Hz for the mu and alpha oscillations frequency band was based on prior research (Haegens et al., 2011; Jurkiewicz et al., 2006; Muthukumaraswamy & Johnson, 2004).

2.3.3 | Principal component analysis (PCA)

To further understand the contribution of mu and alpha oscillations and their proposed functions: mu oscillations reflecting kinaesthetic-based imagery and alpha oscillations reflecting visual-based imagery, we applied a data-driven approach to explore the topographic variability of 8–14 Hz (both mu and alpha frequency band) during successful imagery questions. We evaluated the topographic distribution using principal component analysis (PCA), which has been employed to study the spatial topographic variability of EEG and MEG recordings (Huster et al., 2015; Kovacevic & McIntosh, 2007; Zuure et al., 2020). Frequency-specific P_{episode} (8–14 Hz) was extracted at the trial level (only the correct trials were included), separated by question type (left- and right-hand questions) and averaged within a given recording electrode for a total of 256 electrodes. Each participant had two topographic vectors (2567 electrodes channel × averaged P_{episode} value) during left-hand questions and right-hand questions. We concatenated the topographic vectors across subjects, resulting in four topographic matrices for PCA (LH participants: 256 electrodes × 17 subjects and RH participants: 256 electrodes × 20 subjects). PCA was carried out using the *pca.m* MATLAB function using the default singular value decomposition (SVD) algorithm. We examined the coefficient, spatial distribution, variances and percentage of total variance for every principal component.

3 | RESULTS

3.1 | Behavioural results

We first analysed participants' performance on the task through trial accuracy. The mean score was 15.20

(*SD* = 3.13) out of 20, and when separated by question type (left-hand versus right-hand questions), the mean scores were 7.57 (*SD* = 2.02) out of 10 for right-hand questions and 7.60 (*SD* = 1.89) out of 10 for left-hand questions. Additionally, we separated scores based on the participants' handedness, and the mean scores and their standard deviations are summarised in Table 1. Using a 2-by-2 mixed ANOVA with the within-subjects factor of question type (left-hand versus right-hand questions) and the between-subjects factor of handedness (RH versus LH), no main effect of question type, right-hand question - left-hand question: $F(33, 1) = 0.047$, $p = .830$, and a trending effect of handedness, LH - RH: $F(33, 1) = 3.931$, $p = .056$, were found. A significant interaction between question type and handedness was found, $F(33, 1) = 4.134$, $p = .050$ (Figure 2a). Specifically, using pairwise post hoc comparisons, with p values adjusted for comparing a family of 6, LH participants performed significantly better than the RH participants on the right-hand questions, $t(33) = 2.806$, $p = .040$. There was no significant difference between group performances on the left-hand questions.

To provide further context to these results, we then separated questions according to whether they involved imagery of the participant's dominant- (right-hand questions for RH individuals; left-hand questions for LH individuals) versus non-dominant-hand (left-hand questions for RH individuals; right-hand questions for LH individuals). We used a 2-by-2 mixed ANOVA with the within-subjects factor of question type (dominant-hand question versus non-dominant-hand question) and the between-subjects factor of handedness (RH versus LH). We found a small main effect of question type, non-dominant - dominant-hand questions, $F(33, 1) = 4.134$, $p = 0.050$, and the same small trending effect of handedness, LH - RH, $F(33, 1) = 3.931$, $p = 0.056$. In particular, both groups performed slightly better on questions that involved imagery of non-dominant-hand movements.

Next, we examined participants' response time (RT) on the task questions (summarised in Table 2) using a 2-by-2-by-2 mixed ANOVA with the within-subject factors of question type (dominant-hand question versus non-dominant-hand question) and accuracy (correct versus incorrect) and the between-subject factor of handedness (LH versus RH). A main effect of accuracy was found, where participants responded more quickly on correct trials than on incorrect trials, $F(1, 22) = 13.906$, $p = 0.001$, but no main effect of question type was found (dominant-hand question to non-dominant-hand question: $F(1, 22) = 0.301$, $p = .589$. There was no significant between-subject effect of handedness, $F(1, 22) = 0.867$, $p = .362$, and no significant interactions amongst these factors. When separated by question type and handedness, using pairwise post hoc comparisons, with the p value adjusted for comparing a family of 6, we found significant RT differences for correct and incorrect responses for both dominant- and non-dominant-hand questions. Specifically, there was a significant RT difference between correct and incorrect trials for dominant questions, Correct - Incorrect: $t(41.67) = -3.990$, $p = .002$, and non-dominant questions, Correct - Incorrect: $t(41.67) = -3.125$, $p = .019$ (Figure 2b). In short, participants were faster in responding to correct imagery trials.

3.2 | Oscillation results

We examined mu and alpha activity, detected with the BOSC method, to test our hypothesis. Oscillations were quantified using P_{episode}, a proportional duration measure. It is a measure of duration rather than power and therefore is sensitive to how long a rhythm lasts, but relatively insensitive to the rhythm's amplitude. A P_{episode} value of 0.1 indicates that oscillations at the given frequency were present during 10% of the recording time (Chen & Caplan, 2017; Hughes et al., 2011; Whitten et al., 2011). We were interested in the sustained mu oscillations at the motor electrode cluster (C3, C4 and Cz) for mu oscillations and alpha oscillations at the occipital electrode cluster (O1, O2 and Oz) during the entire imagery time window. In other words, whether the presence or the absence of given oscillations may relate to imagery success. The oscillation measure is shown in Figure 3a for both motor and occipital electrode clusters, and their mean P_{episode} and their standard deviations are summarised in Table 3. A 2-by-2-by-2 mixed ANOVA with the within-subjects factor of question type (right-hand question versus left-hand question), electrode location (motor versus occipital) and the between-

TABLE 1 Participants' scores on the Test of Ability in Movement Imagery–Hand (TAMIh) and their standard deviations.

	TAMIh score (total = 20)	TAMIh right-hand questions (total = 10)	TAMIh left-hand questions (total = 10)
Right-handers	14.3 (3.3)	6.8 (2.1)	7.5 (2.1)
Left-handers	16.3 (2.5)	8.6 (1.4)	7.7 (1.6)

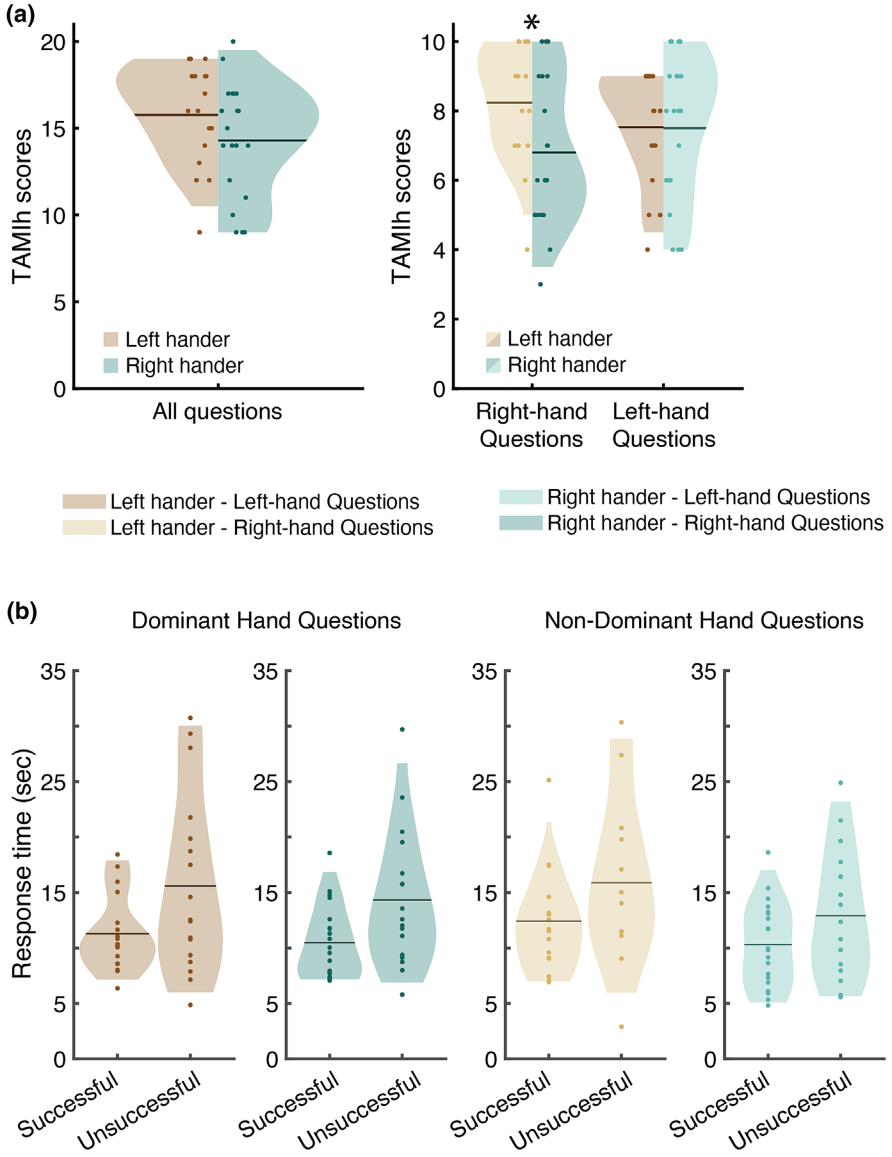

FIGURE 2 Distribution of participants' scores and response times on the imagery task. (a) Task scores are shown for left- and right-handers on all questions and for left- and right-hand movement questions. Statistical analyses revealed that left-handers scored higher on the overall task and on right-hand movement questions. (b) TAMIh response times for successful and unsuccessful trials are shown for left- and right-handers on dominant- and non-dominant-hand questions. Statistical analysis revealed that participants responded significantly faster to successfully imagined movements for both question types.

TABLE 2 TAMIh response time (ms) value reported along with their standard deviations across participants separated by question type, accuracy and participant handedness.

	TAMIh all questions		TAMIh right-hand questions		TAMIh left-hand questions	
	Correct	Incorrect	Correct	Incorrect	Correct	Incorrect
Right-handers	10,367 (3320)	13,186 (5225)	10,482 (3298)	14,331 (6215)	10,316 (3796)	12,913 (5828)
Left-handers	12,040 (3777)	15,079 (7115)	12,563 (4867)	16,438 (8413)	11,407 (3675)	15,785 (8511)

subjects factor of handedness (RH versus LH) revealed a significant main effect of electrode location, occipital - motor: $F(1, 1) = 5.650$, $p = .023$. No main effect was found for question type, $F(35, 1) = 0.503$, $p = .483$ or handedness, $F(35, 1) = 0.013$, $p = .909$. A significant interaction of electrode location, handedness and question type was found, $F(35, 1) = 4.911$, $p = .033$. Specifically, pairwise post hoc comparisons, with p value adjusted for comparing a family of 4, LH showed a significant difference between motor and occipital oscillatory activity for the right-hand (non-dominant-hand) questions, occipital - motor: $t(43.134) = 2.106$, $p = .041$, but not for left-hand (dominant-hand) questions, occipital - motor: $t(43.134) = 0.76$, $p = .637$, whereas RH participants showed a significant difference between motor and occipital oscillatory activity for left-hand

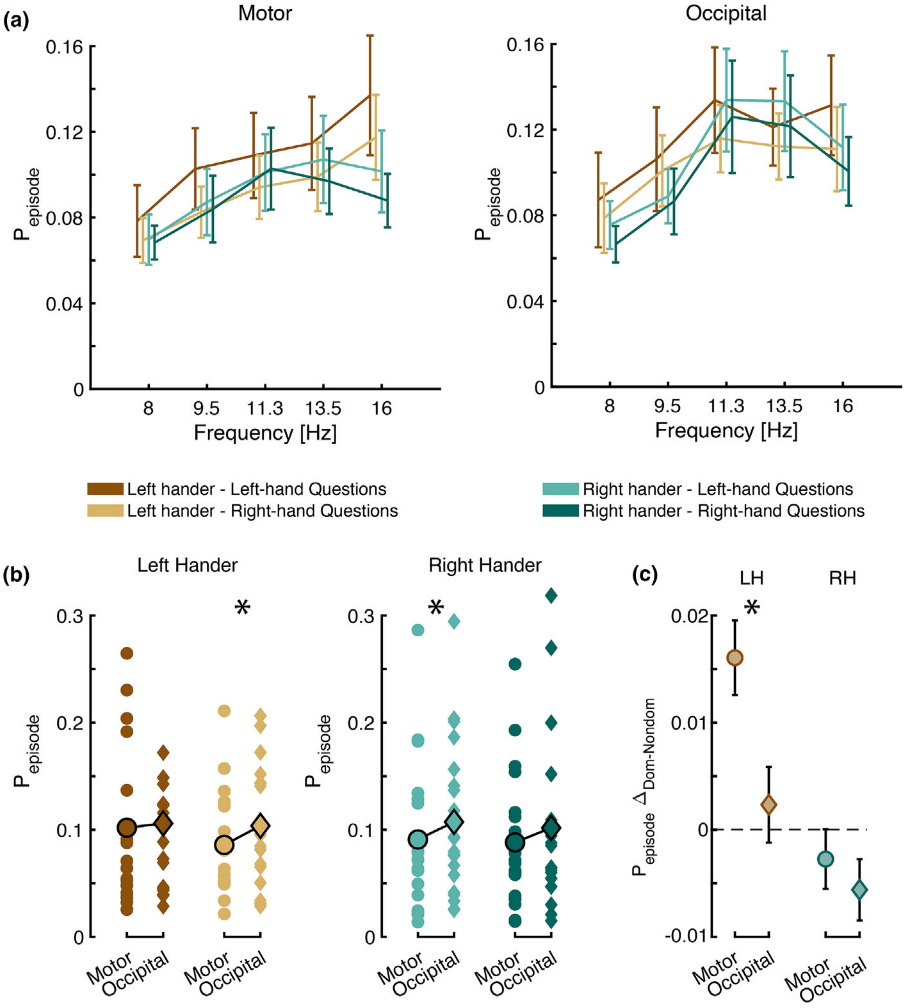

FIGURE 3 Oscillatory activity and handedness. (a) Group averaged oscillatory activity measured by P_{episode} during successfully imagined left- and right-hand movement for left- and right-handers over motor and occipital regions for mu and alpha frequency bands. (b) Comparison between averaged mu-band activity at motor and averaged alpha-band activity at occipital regions during successfully imagined left- and right-hand movement for left- and right-handers. (c) P_{episode} difference between successfully imagined dominant- versus non-dominant-hand movements for left- and right-handers for mu-band activity at motor regions and alpha-band activity at occipital regions. (* denotes $p < 0.05$ significance).

TABLE 3 Mean P_{episode} value reported along with their standard deviations across participants separated by question type, cluster location, and participant handedness.

	TAMIh right-hand questions		**TAMIh left-hand questions**	
	Motor	**Occipital**	**Motor**	**Occipital**
Right-handers	.088 (.062)	.102 (.079)	.091 (.067)	.107 (.072)
Left-handers	.086 (.050)	.104 (.057)	.102 (.079)	.106 (.079)

(non-dominant-hand) questions, occipital - motor: $t(43.134) = 2.094$, $p = .042$, but not for right-hand (dominant-hand) questions, occipital - motor: $t(43.134) = 1.739$, $p = .089$. In sum, there was a significant difference between motor and occipital oscillatory activity when participants imagined movements with their non-dominant hand (Figure 3b).

To further understand the main driver of the significant differences we observed between motorversus occipital regions, we included two additional analyses. First, we examined the oscillatory activity difference ($\Delta_{(\text{dominant} - \text{non-dominant})}$) when participants were imagining dominant- versus non-dominant-hand movements (i.e., left-hand minus right-hand movements for LH participants and right-hand minus left-hand movements for RH participants). This difference measure would help to identify the region that drives the observed differences in oscillatory activity. Using this $\Delta_{(\text{dominant} - \text{non-dominant})}$ difference measure, we compared activity between motor and occipital regions and found a significant difference in LH participants, motor - occipital: $t(16) = 2.204$, $p = .043$, but not in RH participants, $t(19) = 0.631$, $p = .536$, as shown in Figure 3c. In short, the significant difference between motor and occipital region during non-dominant movement were driven by different factors for LH and RH participants. This result may suggest a possible shift in cognitive strategies in LH participants when imagining familiar (dominant) and unfamiliar (non-dominant) movements.

Second, mu and alpha oscillations share a similar frequency range; however, their topographic distributions differ spatially. Mu oscillations are commonly reported over the central motor regions, whereas alpha oscillations are often observed over the occipital region. While the electrodes were selected for mu and alpha oscillations analysis based on prior work, it was still difficult to disentangle the contribution of mu and alpha oscillations and the imagery strategies that these two rhythms may index during TAMIh for participants' dominant and non-dominant hands. Therefore, we employed a data-driven approach to explore the possible spatial features of the 8–14 Hz frequency band (for both mu and alpha oscillations). Specifically, we were interested in the most salient topographical features identified by applying principle component analysis (PCA) to the topographic distribution during successful imagery of left- and right-hand movements for LH participants and RH participants (Figure 4). For LH participants, during their non-dominant-hand (right-hand) movement, the first principle component explained 44.44% of the variance and displayed a strong occipital spatial feature (Figure 4a). The first five components explained more than 80% of the variance (II: 16.37%, III: 11.53%, IV: 6.29% and V: 4.83%, Figure 3a). For RH participants, during their non-dominant-hand (left-hand) movement, the first principle component explained 28.16% of the variance and displayed a strong occipital spatial feature (Figure 4b). The first five components explained more than 80% of the variance (II: 18.80%, III: 15.42%, IV: 10.71% and V: 7.16%, Figure 3b). For LH individuals, during their dominant-hand (left-hand) movement, the first principle component explained 35.84% of the variance and displayed a bilateral central/occipital spatial feature (Figure 4c). The first five components explained more than 80% of the variance (II: 22.29%, III: 10.26%, IV: 7.11% and V: 4.99%, Figure 4c). For RH participants, during their dominant-hand (right-hand) movement, the first principle component explained 40.12% of the variance and displayed an occipital spatial feature (Figure 4d). The first five components explained more than 80% of the variance (II: 16.09%, III: 12.99%, IV: 8.93% and V: 4.91%, Figure 3d). Salient topographical features of other principle components (II to IV) did not display a coherent spatial pattern as illustrated in the top component for each condition.

4 | DISCUSSION

The present study investigated imagery of fine motor movements in RH and LH individuals, with a particular focus on dominant- versus non-dominant-hand movements. Results demonstrated similarities and differences between groups. Behaviourally, LH participants were more accurate on right-hand questions than RH participants, with both groups performing significantly better on questions that involved their non-dominant hand. Across participants, reaction time was shorter during trials that

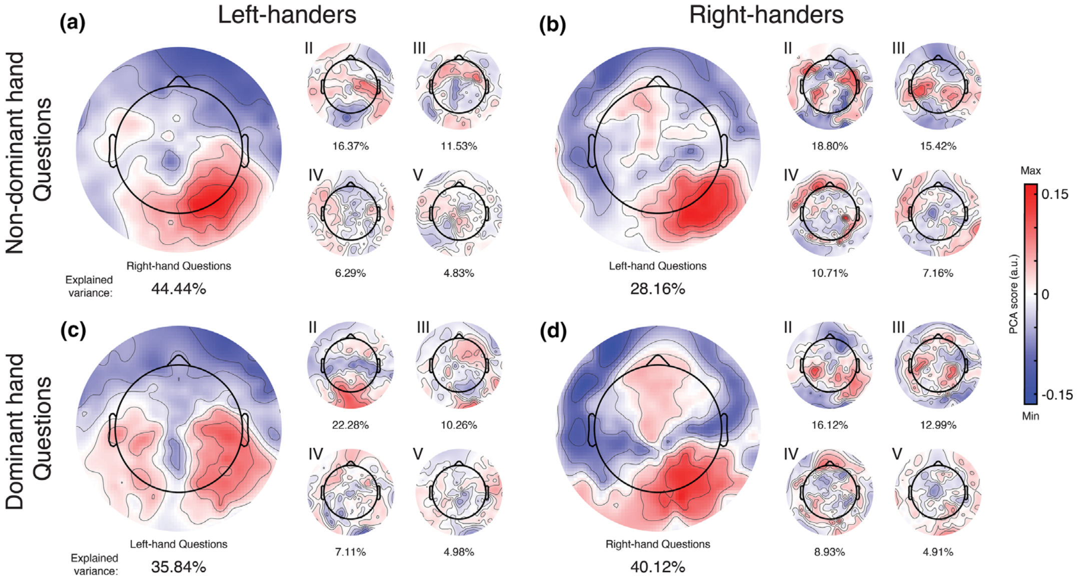

FIGURE 4 Topographies capturing principal component analysis (PCA) salient spatial feature and the percentage of variance explained by each component across left- and right-handers during successful imagery of their dominant- and non-dominant-hand questions.

resulted in a correct response. On an electrophysiological level, both LH and RH participants displayed a significant difference in oscillatory activity between motor and occipital regions during imagery during non-dominant-hand movements. For LH participants, this result was primarily driven by differences in mu activity.

Both groups were more accurate on questions that involved the non-dominant hand. This result is somewhat unexpected. RH individuals typically perform better on imagery tasks that involve their dominant hand, while findings in LH individuals are mixed. By definition, individuals predominantly use their dominant hand to carry out daily tasks. The sensorimotor representations of the dominant hand are consequently more developed than those of the non-dominant hand and more easily accessed during motor imagery (Ní Choisdealbha et al., 2011). However, it is possible that these more established representations may then interfere with imagery of less natural actions. Evidence for this theory comes from the hand laterality judgement task, where only imagery of the dominant hand was disrupted in RH individuals when the participant's hand was placed in position posturally incongruent to the imagined action (Conson et al., 2010; Ionta & Blanke, 2009; Jones et al., 2021; Ní Choisdealbha et al., 2011). Greater familiarity with the dominant hand may have therefore exacerbated the complexity of the isolated fine motor movements involved in the TAMIh, leading to a decrease in accuracy.

An alternative explanation to this proposal is that more experience using the dominant hand enabled participants to access the hand's sensorimotor representations of the dominant hand more quickly than those of the dominant hand. This ease of access then led to more rushed processing of the question, resulting in more error-prone responses (Ní Choisdealbha et al., 2011). However, our reaction time results do not support a speed-accuracy trade off. We found no differences in reaction time between dominant- and non-dominant-hand movements. Across conditions, participants took significantly longer to respond to questions that resulted in an incorrect response. Much like their physical performance, more difficult movements also take longer to imagine (McAvinue & Robertson, 2008). Incorrect responses in the current task are therefore likely not a result of rushed processing, but greater difficulty imagining the described movement.

Between-group analyses revealed that LH participants were significantly more accurate than RH participants on right-hand questions of the task. Given the previous results, this finding is not surprising, as right-hand questions involve the non-dominant hand for LH individuals and the dominant hand for RH individuals. Interestingly, no significant differences were observed between participants on left-hand questions. In other words, accuracy in the worse performing condition for LH participants (dominant-hand questions) was equivalent to accuracy in the better performing condition for RH participants (non-dominant-hand questions). This discrepancy may be a consequence of between-group differences in imagery strategy. While instructions were identical between groups, it has previously been suggested that LH individuals and RH individuals use different strategies when completing the same imagery task (Ní Choisdealbha et al., 2011; Zapała et al., 2020).

The EEG data provides a possible explanation for our behavioural results. In LH participants, significant differences between alpha and mu activity occurred only during imagery of right-hand (non-dominant-hand) movements. In particular, less time was occupied by mu oscillations during right-hand imagery, suggesting greater activation of the motor cortices when the imagined movement involved their non-dominant hand. One interpretation is that LH participants adjusted their imagery strategy when imagining movements with their right hand, putting more effort into generating the comparatively unfamiliar kinaesthetic sensations of their non-dominant hand. The PCA results support this interpretation, with observable differences in the principal spatial features of 8–14 Hz activity in LH participants between imagery of left- versus right-hand movements. Zapała et al. (2020) previously reported a lack of mu suppression in LH individuals during imagery of their dominant hand, with their analysis focusing on mu activity in the motor cortex contralateral to the movement being imagined (Zapała et al., 2020). The present work indicates that mu oscillations occupy less time during motor imagery of non-dominant-hand movements in LH individuals across the motor cortex.

RH participants also exhibited significant differences between alpha and mu activity during imagery of their non-dominant hand (left-hand movements). However, a clear shift in strategy cannot be interpreted from the data as the differences in oscillatory activity were not primarily driven by either rhythm. This lack of shift is also present in the PCA results. As compared to LH participants, RH participants did not exhibit observable differences in the spatial features of 8–14 Hz activity between dominant- and non-dominant-hand imagery. The oscillatory differences observed in RH participants could indicate a general adjustment in attentional resources when imagery involves the non-dominant hand, as opposed to a change in imagery strategy.

It is worth noting that the PCA results show that activity in the 8–14 Hz rhythm was most pronounced towards the posterior region of the brain in both groups. This concentration may reflect a dominance of alpha oscillations during the TAMIh. While alpha is primarily known as an inhibitory rhythm, it has previously been proposed that increases in alpha activity reflect a shift from processing external to internal stimuli. We therefore interpret this concentration of alpha activity as reflecting an emphasis placed by participants on mentally generating visual images during the TAMIh. The visual modality is considered easier to use and particularly beneficial during imagery of complex or unfamiliar movements. The imagined movements in the TAMIh are rarely performed in isolation and would therefore be highly unfamiliar to participants. It is therefore unsurprising that participants would primarily rely on the visual modality to respond to the task.

Lastly, research indicates that LH individuals have more flexible mental representations of movement than RH individuals. For example, observing the picture of an action from a perspective that mismatches the observer's own mental simulation of that action disrupts learning in RH individuals (de Nooijer et al., 2013). However, this disruption does not occur in LH individuals. Similarly, a change in the orientation of a tool's handle alters the perceived distance to reach that tool only in RH individuals (Linkenauger et al., 2009). This flexibility is likely a consequence of LH individuals existing in a world designed and used primarily by RH individuals. In the present study, we suspect that LH participants were more prone to adapt their imagery strategy according to task demands, enabling the increased accuracy when executing motor imagery of right-hand movements.

There are some key limitations to the present work. First, we did not use electromyographic (EMG) recordings during data collection. Participants were instructed not to move during the imagery task and only imagine the movement commands displayed on screen. While we are confident that voluntary movements did not impact the recordings, the same cannot be confirmed for subthreshold motor activation. As our interest was to compare imagery of dominant- and non-dominant-hand movements in right versus LH participants, we did not include a baseline control condition. While we suspect that participants primarily engaged the visual modality during the imagery task, an increase in occipital alpha as compared to the baseline condition would provide additional support for this theory. Given that participants held a tennis ball in the target hand, we also cannot rule out the possibility that participants exhibited differences in alpha activity when anticipating a dominant- versus non-dominant-hand question. Such differences could impact the patterns of oscillatory activity observed during the imagery process.

In conclusion, this study provides new insight into the effect of hand dominance on the mental representation of movement. We have shown that both RH and LH individuals imagine movements differently when it involves their dominant versus non-dominant hand. In LH participants, this difference may reflect a shift in imagery strategy that involves increased recruitment of the kinaesthetic modality during imagery of the non-dominant hand, a finding further supported by the spatial distribution of rhythmic activity captured through PCA. No clear differences in activity were observed between dominant- and non-dominant-hand questions in RH participants, who performed less accurately on right-hand questions. These results suggest that LH individuals may have more flexible mental representations of movement than RH individuals. An interesting question for future research would be to examine if our oscillation results extend to imagery of more familiar movements or movements that involve tools.

AUTHOR CONTRIBUTIONS

Kathryn J. M. Lambert: Data curation; formal analysis; visualisation; writing—original draft; writing—review and editing. **Yvonne Y. Chen**: Data curation; formal analysis; visualisation; writing—original draft; writing—review and editing. **Christopher Donoff**: Conceptualisation; data curation; investigation; project administration. **Jonah Elke**: Conceptualisation; investigation; writing—review and editing. **Christopher R. Madan**: Conceptualisation; methodology; software; supervision; writing—review and editing. **Anthony Singhal**: Conceptualisation; funding acquisition; methodology; resources; supervision; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Study data is available in the University of Alberta Dataverse, which is hosted on the Borealis data repository. The dataset can be accessed at this Additional questions regarding the study can be directed to the corresponding author.

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