Received: 3 March 2022 | Revised: 12 August 2022 | Accepted: 17 August 2022

DOI: 10.1111/psyp.14179

PSYCHOPHYSIOLOGY SPR WILEY

ORIGINAL ARTICLE

# Neural basis of implicit motor sequence learning: Modulation of cortical power

**Jarrad A. G. Lum**[1] | **Gillian M. Clark**[1] | **Pamela Barhoun**[1] | **Aron T. Hill**[1] | **Christian Hyde**[1] | **Peter H. Wilson**[2,3]

[1]School of Psychology, Cognitive Neuroscience Unit, Deakin University, Burwood, Victoria, Australia

[2]School of Behavioural and Health Sciences, Australian Catholic University, Melbourne, Victoria, Australia

[3]Healthy Brain and Mind Research Centre, Melbourne, Victoria, Australia

**Correspondence**
Jarrad A. G. Lum, School of Psychology, Deakin University, 221 Burwood Highway, Burwood, VIC 3125, Australia.
Email: jarrad.lum@deakin.edu.au

## Abstract

Implicit sequence learning describes the acquisition of serially ordered movements and sequentially structured cognitive information, that occurs without awareness. Theta, alpha and beta cortical oscillations are present during implicit motor sequence learning, but their role in this process is unclear. The current study addressed this gap in the literature. A total of 50 healthy adults aged between 19 and 37 years participated in the study. Implicit motor sequence learning was examined using the Serial Reaction Time task where participants unknowingly repeat a sequence of finger movements in response to a visual stimulus. Sequence learning was examined by comparing reaction times and oscillatory power between sequence trials and a set of control trials comprising random stimulus presentations. Electroencephalography was recorded as participants completed the task. Analyses of the behavioral data revealed participants learnt the sequence. Analyses of oscillatory activity, using permutation testing, revealed sequence learning was associated with a decrease in theta band (4–7 Hz) power recorded over frontal and central electrode sites. Sequence learning effects were not observed in the alpha (7–12 Hz) or beta bands (12–20 Hz). Even though alpha and beta power modulations have long been associated with executing a motor response, it seems theta power is a correlate of sequence learning in the manual domain. Theta power modulations on the serial reaction time task may reflect disengagement of attentional resources, either promoting or occurring as a consequence of implicit motor sequence learning

**KEYWORDS**

alpha, beta, electroencephalography (EEG), implicit motor sequence learning, neural oscillations, serial reaction time (SRT) task, theta

## 1 | INTRODUCTION

Implicit sequence learning describes the acquisition of skills and knowledge, generated by repeatedly executing or processing serially ordered movements or percepts (e.g., Fiser & Aslin, 2002; Isbilen et al., 2020; Nissen & Bullemer, 1987; Saffran et al., 1997). The learning is implicit since the performer develops no reportable awareness of the dependencies between sequence elements (Cleeremans et al., 1998; Lewicki et al., 1988). Implicit sequence learning is fundamental to a range of human abilities (e.g., motor function, language, social interaction) (Clegg et al., 1998; Hamrick et al., 2018) and is impaired in a number of neurodevelopmental, neurodegenerative and psychiatric disorders (Clark & Lum, 2017). Neuroimaging studies suggest this type of learning, at least in the motor domain, activates a basal ganglia-cortical network that includes the striatum, prefrontal cortex, primary motor cortex, supplemental motor area and possibly medial temporal lobe (Albouy et al., 2008; Hardwick et al., 2013; Janacsek et al., 2020; Pascual-Leone et al., 1996; Schendan et al., 2003). Much less is known about the role of neural oscillatory activity, which enables information transfer and processing in the brain (Başar et al., 2001; Ward, 2003), during implicit motor sequence learning. Addressing this gap in the literature is needed to understand a critically important learning mechanism, and its genesis of impairment in a number of disorders.

Cycles of synchronized-desynchronised activity of summed dendritic post-synaptic potentials generates oscillatory activity in the brain, leading to rhythmic fluctuations in the amplitude of the electroencephalogram (EEG) and magnetoencephalogram (MEG) (Jackson & Bolger, 2014; Nunez & Srinivasan, 2006). Oscillatory activity is also generated by subcortical structures that comprise the basal ganglia, but is unlikely to be detected by scalp electrodes (Cohen et al., 2011). In general, as more neurones are synchronously activated, the amplitude of the M/EEG increases. In the mammalian brain, oscillatory activity occurs within bands of approximately 1–4, 4–8, 8–12, 12–30 and 30–100 Hz termed delta, theta, alpha, beta and gamma, respectively (Buzsáki et al., 2013).

Oscillatory activity during implicit motor sequence learning has mainly been examined using the serial reaction time (SRT) task (Heideman et al., 2018; Meissner et al., 2018, 2019; Pollok et al., 2014; Tóth et al., 2017; Tzvi et al., 2016; Zhuang et al., 1997). On this task a visual stimulus appears repeatedly in one of four (or more) visual spatial locations on a computer display (Nissen & Bullemer, 1987). The stimulus prompts participants to press one of four buttons on a response panel that matches the stimulus' location. Participants are not informed that the trial-to-trial location of the visual stimulus follows a repeating, pre-determined order. In healthy controls, manual reaction times decrease (i.e., become faster) across trials as the sequence of finger movements is unknowingly repeated. Faster reaction times partially occur because the location of an upcoming visual stimulus is predicted (without awareness) by the manual response system (Lum, 2020; Robertson, 2007). This pattern of implicit learning is highlighted following introduction of a control block of trials presented at the end of the task, in which the visual stimulus appears randomly in one of the predefined locations. On this part of the task, reaction times increase (i.e., become slower) because the stimulus' location can no longer be predicted (e.g., Deroost et al., 2006; Lukács & Kemény, 2015; Lum, 2020; Lum et al., 2019; Nissen & Bullemer, 1987; Thomas et al., 2004; Thomas & Nelson, 2001). General motor learning may also contribute to faster reaction times on the SRT task. General motor learning occurs as stimulus–response associations are strengthened, that is, mapping a motor response to a specific visuo-spatial location. This type of learning is revealed by faster reaction times on random trials of the SRT task where the visual stimulus appears in non-predictable locations (Marcus et al., 2006).

Performance on the SRT task has been shown to modulate oscillatory power in beta, alpha and theta bands (Heideman et al., 2018; Meissner et al., 2018, 2019; Pollok et al., 2014; Tzvi et al., 2016; Zhuang et al., 1997). At present, it is unclear whether these modulations support sequence learning or general motor learning effects. One hypothesis is that beta oscillations may reflect cortical reorganization associated with sequence learning (Pollok et al., 2014, 2015). Beta desynchronisation, that is reduced beta power, not only supports execution of movement (Pfurtscheller & Da Silva, 1999), but has been proposed to permit bottom-up or sensory-driven information to modify current performance or motor programs (Engel & Fries, 2010). On the SRT task, beta desynchronisation may promote plasticity within the primary motor cortex, enabling motor programs, or engrams, to be updated as the sequence is repeated. Thus, on this task, beta power should be lower on sequence trials compared with random trials; a result observed by Heideman et al. (2018). Further evidence for a role of beta oscillations in implicit sequence learning was observed by Meissner et al. (2018). In that study, beta power over the primary motor cortex was found to be lower in healthy controls who implicitly learnt a motor sequence, compared to participants with Parkinson's disease who evidenced lower levels of learning. Not all studies, however, provide unequivocal support for an association between beta oscillations and implicit sequence learning. Pollok et al. (2014) found no difference in beta power between sequence and random trials on the SRT task.

Further correlation analyses, however, did reveal an association between beta desynchronisation and sequence retention. This potentially suggests oscillatory activity in this frequency band may play a role in the long-term storage of the sequence, rather than learning.

Alpha power is also modulated during implicit motor sequence learning. Several studies using the SRT task have found alpha power, recorded over the primary motor cortex and parietal-occipital lobe (Pollok et al., 2014; Tzvi et al., 2016; Zhuang et al., 1997), to be higher on sequence trials compared with random. Localized increases in alpha power have an inhibitory effect on cortical functioning. This is often observed when a region of the brain is no longer involved in completing a task (Klimesch et al., 2007; Pfurtscheller, 1992, 2001). Sequence learning may enable manual responses to be executed in an increasingly automatic manner, thereby reducing the cortical resources needed to monitor and then respond to a visual stimulus (Lum et al., 2019; Thomas et al., 2004; Zhuang et al., 1997). On the SRT task, alpha power should therefore be higher on sequence trials compared to random. Not all study findings are consistent with this position. Tzvi et al. (2016) found that after sequence learning, alpha power was higher on random trials compared to sequence.

Finally, inconsistencies in the literature have emerged with respect to theta power. Meissner et al. (2018), described above, found that in healthy controls, who implicitly learnt a motor sequence, theta power over the primary motor cortex was higher on sequence trials compared to random. This difference was reduced in the participants with Parkinson's disease, who evidenced impaired sequence learning abilities. An additional analysis revealed a positive correlation between theta power and sequence learning, but only in the group with Parkinson's disease. These results may be indicating that increases in theta power promote sequence learning. Interestingly, increases in theta power also occur during explicit motor learning (Rozengurt et al., 2016; van der Cruijsen et al., 2021). One potential caveat to Meissner et al.'s (2018) findings is that, abnormal theta oscillatory activity appears to be part of broader brain and cognitive dysfunction in Parkinson's disease (Geraedts et al., 2018). Differences in theta power on the SRT task between control and Parkinson's disease groups, might be related to non-specific effects of neurodegeneration on neural functioning, rather than sequence learning related oscillatory activity. Alternatively, theta power changes across the SRT task may be more related to generating a motor response, than sequence learning. That is, learning and/or executing stimulus–response associations. Tzvi et al. (2016) found that as more trials were completed on the SRT task, theta power decreased irrespective of whether a sequence or random motor response was generated.

### 1.1 | The current study

The aim of the current study was to examine oscillatory activity during implicit motor sequence learning. In this study, healthy adults completed an SRT task. Both manual responses and EEG were recorded. The task consisted of seven blocks of trials. The first and last block (i.e., Block 1 & 7) comprised random trials and the remaining blocks (Blocks 2–6), sequence trials. The presence of sequence learning effects in oscillatory power and also manual responses were tested by contrasting data between the final random block and preceding sequence block (i.e., Block 6 & 7). This contrast is commonly used to test sequence learning effects in behavioral and neuroimaging (fMRI/PET) data on the SRT task, since it controls for the effects of general motor (i.e., stimulus response learning) learning (Clark & Lum, 2017; Hardwick et al., 2013; Janacsek et al., 2020; Janacsek & Nemeth, 2013; Lum, 2020; Robertson, 2007). This specific comparison has not been tested in most past studies examining oscillatory activity on this task (Heideman et al., 2018; Meissner et al., 2018; Pollok et al., 2014). Thus, reported beta, alpha and/or theta power modulations previously observed on the SRT task, might not reflect sequence learning related brain activity. This possibility was also examined in the current study. General motor learning, which primarily encompasses learning stimulus–response associations, was examined by comparing differences in the data between the first and final random block (i.e., Block 1 & 7). Both blocks comprised random trials, thus potential differences in the data on this comparison would indicate improvements associated with providing a manual response to non-predictable stimulus presentations.

## 2 | METHOD

### 2.1 | Participants

A total of 50 healthy adults (33 female, 17 male) aged between 19.4 and 37.2 years ($M = 24.0$, $SD = 3.8$) participated in the study. Power analysis indicated a sample size of 50 participants provided a 90% chance of detecting a standardized mean difference of 0.5 between the random and sequence blocks. This corresponds to a medium effect size in Cohen's taxonomy (Cohen, 2013). The sample were predominantly right-handed. Handedness was screened using the Edinburgh Handedness Inventory (Oldfield, 1971). This instrument was scored on a range of −100 to 100 where positive values indicate a tendency for right handedness and negative values, left handedness. The mean handedness score for the sample was 61.7 ($SD = 57.9$; Range: −100 to 100) and there were

43 participants with positive values (indicating right-handedness). Almost all the sample held a university/college degree ($n = 45$). Written consent was obtained before taking part in the study. The study was approved by the Deakin University Human Research Ethics Committee and research protocols adhered to the Declaration of Helsinki (World Medical Association, 2001). All participants were provided with a $30 shopping voucher for taking part in the study.

## 2.2 | Materials

### 2.2.1 | Serial reaction time task

Participants were administered a version of Nissen and Bullemer's (1987) SRT task. Participants completed seven blocks of 60 trials. Each trial commenced with a blank screen (colored gray) for 500 ms. A visual stimulus then appeared in one of four horizontal positions for 650 ms. The only instruction provided to participants was to press one of four horizontally arranged buttons on a response panel, that matched the visual stimulus' location. All participants operated the response panel using their right hand. Specifically, the 2nd through to 5th digit was used to press the left- to right-most buttons respectively. During testing, participants rested each finger on separate buttons. Participants could respond anytime during the 650 ms period. For responses made before 650 ms, the visual stimulus would stay on screen for the remaining time. For example, if the participant made a response 400 ms, post stimulus onset, the visual stimulus would stay on the screen for a further 250 ms. This was also the case when participants pressed a button on the response panel that did not match the stimulus' location. Figure 1 summarizes the trial design.

Participants were unaware that on Blocks 2–6, hereafter referred to as the 'sequence blocks', the visual stimulus' location on each trial followed a pre-determined 10 element sequence. Labelling the left-most position on the computer display that the visual stimulus could appear as 1, and right-most 4, the sequence was 3-4-1-2-4-1-3-4-2-1. This is a first order conditional sequence, in which each element in the sequence is predictive of the next. For example, spatial position '3' in the sequence is always followed by position '4'. It has been suggested this type of sequence is specifically processed by the basal ganglia procedural memory system (Poldrack & Rodriguez, 2003). On Blocks 1 and 7, hereafter referred to as the 'random blocks', the visual stimulus appeared pseudo-randomly in one of four positions on the display adhering to the following three constraints. First, the visual stimulus could not appear in the same location on two consecutive trials. Second, the number of times the visual stimulus appeared in each of the four spatial locations was the same as for the sequence blocks. For example, on each sequence block the visual stimulus appeared in Position 1, a total of 18 times. This was also the case for the random blocks. Third, the frequency of each pairwise transition in the random blocks matched the sequence blocks. For example, on each sequence block, the visual stimulus moved from Position 3 to Position 4 a total of 20 times. This was also the case on the random blocks. Unlike the sequence blocks, however, these pairwise transitions did not occur within a sequence. Thus, potential differences in the data between sequence and random blocks is unlikely to be due to participants only learning pairwise transitions. Finally, the order of random stimulus presentations on Block 1 and Block 7 differed.

The version of the SRT task used in the current study differed from the standard version (Nissen & Bullemer, 1987). First, there were no boxes on the display indicating visual stimulus' locations. Second, a different

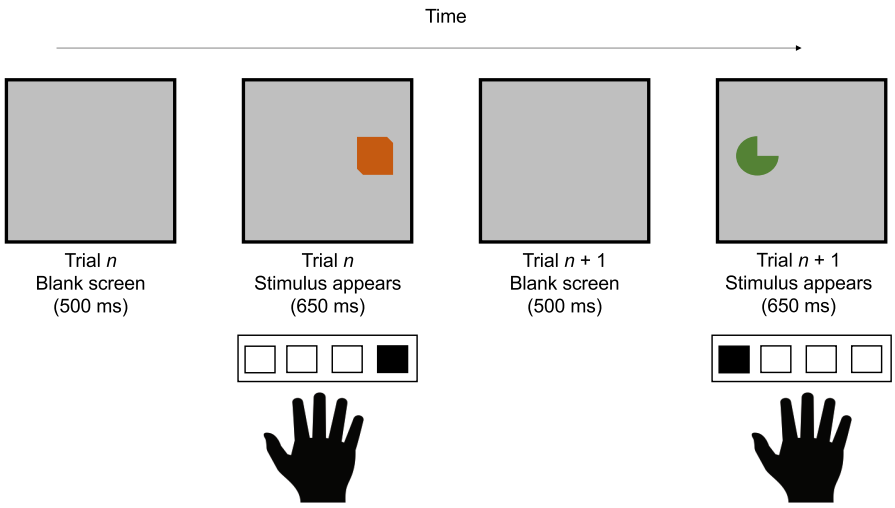


**FIGURE 1** Schematic representation of two trials from the serial reaction time task. Note the stimulus remained on screen for 650 ms irrespective of whether a correct, incorrect, or no response was made during that time

visual stimulus appeared on each trial within a block. The stimuli comprised 60 different shapes (circles and polygons) presented in different colors (purple, green, blue, red, orange). Each stimulus subtended approximately 4.6° × 4.6° of visual angle. On each trial within a block, a visual stimulus was randomly selected without replacement. Thus, on each block the order that the 60 visual stimuli were presented differed. These modifications make it less likely that participants become aware of the sequence (Koch et al., 2020; Lum, 2020). The SRT task was presented using E-Prime 2 software (Psychology Software Tools, Pittsburgh, PA).

Participants' performance on the SRT task was measured by accuracy and reaction times. A correct response was recorded when participants pressed the button on the response pad that matched the visual stimulus' location on the display. All other responses were recorded as incorrect. Failure to provide a manual response to the visual stimulus within 650 ms was also coded as an incorrect response. Inspection of the accuracy data indicated participants were consistently responding appropriately to the visual stimulus across all blocks. The proportion of correct responses on each block approached ceiling (Block 1: $M = 0.89$, $SD = 0.11$; Block 2: $M = 0.88$, $SD = 0.08$; Block 3: $M = 0.92$, $SD = 0.08$; Block 4: $M = 0.91$, $SD = 0.09$; Block 5: $M = 0.92$, $SD = 0.08$; Block 6: $M = 0.91$, $SD = 0.09$; Block 7: $M = 0.90$, $SD = 0.09$). Reaction times recorded the time taken to provide a manual response following stimulus onset. Only reaction times associated with a correct response were included in the analyses. For each participant the mean reaction time for each block was computed. These data were submitted for analyses.

### 2.2.2 | EEG acquisition

EEG were continuously recorded using a 25-channel montage as participants completed the SRT task. Events were inserted into the EEG data marking stimulus and manual response onset. EEG was acquired using a TMSi RefA biosignal amplifier (Twente Medical Systems International, The Netherlands) via Ag-AgCl electrodes embedded into an elastic cap (Easycap, Herrsching, Germany). The data were acquired at a sampling rate of 2048 Hz with the common average used as the online reference. The electrodes were placed in positions Fp1, Fp2, F7, F3, Fz, F4, T7, C3, Cz, C4, T8, P7, P3, Pz, P4, P8, O1, O2, M1 (left mastoid) and M2 (right mastoid). Additional electrodes were placed on the left and right outer canthus as well as above and below the left eye to record blinks and eye-movements. Impedances were reduced to less than 5 kΩ before recording commenced.

## 2.3 | Procedure

Participants were individually tested in a laboratory setting. They first completed a background survey and handedness inventory. After the EEG cap and electrodes were fitted, the SRT task was administered. To administer the task, participants first completed 10 practice trials to ensure they understood the mapping between visual stimulus locations and manual responses. The test trials, comprising the seven blocks, were then presented. At the conclusion of the task, participants were asked if they were aware of a sequence or pattern. All the participants included in this study indicated they were unaware that a sequence was present.

## 2.4 | EEG offline pre-processing and time-frequency analysis

All processing of the EEG data were undertaken using the EEGLab Toolbox (Delorme & Makeig, 2004) and MATLAB scripts (Version 2021a; MathWorks, Natick, MA, USA) adapted from Cohen (2014). A 0.1 Hz high pass FIR filter was first applied to the data before down sampling to 500 Hz. Line noise was then removed using a 50 Hz notch filter followed by a 40 Hz lowpass FIR filter. Consistent with most previous research in this field, the continuous EEG were segmented into response-locked epochs (Heideman et al., 2018; Meissner et al., 2018, 2019; Pollok et al., 2014). Each epoch commenced 1000 ms before a manual response was made and ended 1000 ms after. The main analyses examined oscillatory power associated with ±500 ms of data surrounding each manual response. The data were segmented using a larger temporal window to avoid edge artifacts associated with time-frequency decomposition (described below). Channels with excessive noise were identified and then interpolated (via spherical interpolation) using EEGLAB's pop_rejchan (threshold set at 5σ using kurtosis method) and pop_interp functions respectively. The data were then re-referenced to the average of the mastoid electrodes. Blinks and eye-movements were identified for removal using Independent Components Analysis run in EEGLAB (using the RUNICA algorithm) and ADJUST (Mognon et al., 2011). Finally, epochs with a data point exceeding ±80 μV or associated with an incorrect manual response were excluded from further analysis. The average number of epochs, out of a maximum of 60, included in the final analyses are as follows: Block 1: $M = 51.0$ ($SD = 6.6$), Block 2: $M = 50.2$ ($SD = 4.9$), Block 3: $M = 52.5$ ($SD = 5.2$), Block 4: $M = 51.1$ ($SD = 4.6$), Block 5: $M = 52.5$ ($SD = 5.1$), Block 6: $M = 51.9$ ($SD = 5.5$), Block 7: $M = 52.4$ ($SD = 4.7$).

Oscillatory power from the EEG signal was extracted via time-frequency decomposition using complex Morlet wavelets defined as:

$$e^{i2\pi ft}e^{-t2/(2\sigma^2)},$$

whereby frequency ($f$) ranged from 1 to 30 Hz, in 60 logarithmically spaced steps. The width of the wavelet ($\sigma = n / [2\pi f]$) was defined in cycles ($n$), ranging from 2 to 15 logarithmically spaced steps which provided reasonable frequency and temporal resolution. For each participant, trial (or epoch level) time-frequency data were averaged separately for each block and channel. After time-frequency decomposition, the data were further down sampled to 250 Hz in order to decrease the computational time associated with the statistical analyses (described below). The initial result of Morlet wavelet convolution was oscillatory power computed in $\mu V^2$, but in a further step, data were decibel baseline corrected using the average power of the entire epoch. The final data analyzed were the change in oscillatory power from this baseline period, expressed in dB. This approach has previously been used to examine oscillatory activity on the SRT task (Meissner et al., 2018; Pollok et al., 2014). This type of correction was applied because on this task, there are no identifiable rest periods between trials which can be used to define a baseline period; the end of one trial, marks the start of the next. Figure 2 presents baseline corrected power data averaged over all trials, blocks and participants at each electrode site.

## 2.5 | Data analysis

The behavioral data analyzed were manual reaction times. The EEG data analyzed were oscillatory power, between 1 to 30 Hz, occurring ±500 ms around each manual response. In order to reduce the number of statistical tests, time-frequency data were averaged across sets of electrodes which are depicted in Figure 3. A frontal electrode grouping was created by averaging data from electrodes F3, Fz and F4. A central electrode grouping was created by averaging time-frequency data from C3, Cz and C4. Finally, a parietal-occipital grouping was created by averaging data from electrodes P3, Pz, P4, O1 and O2. This grouping of electrodes was based on the results of previous studies that have found oscillatory power in one or more of these groupings is modulated during implicit motor sequence learning (e.g., Frontal: Tzvi et al., 2016; Central: Meissner et al., 2018; Parietal-Occipital: Tzvi et al., 2016). Data from lateral electrodes (e.g., F7/F8, T7/T8) were excluded from the analyses to reduce the influence of muscle related artifacts on the data.

Manual reaction times were analyzed using a one-way repeated measures ANOVA that tested the effect of Block (Block 1, Block 2, Block 3, Block 4, Block 5, Block 6 & Block 7) on reaction times. A significant main effect of Block was then explored using two planned comparisons or contrasts. One contrast examined the presence of sequence learning effects, and the other, general motor learning effects (i.e., stimulus–response learning). The sequence learning contrast tested for differences between Block 6 (sequence trials) and Block 7 (random trials). The general motor learning contrast tested for differences in the data between Block 1 (random trials) and Block 7 (random trials). Each contrast was tested using a paired samples $t$-test. For these analyses, $p$-values were corrected using the Bonferroni Procedure.

Time-frequency data were also analyzed with two contrasts that examined sequence learning and general motor learning effects in oscillatory power. Each contrast was computed separately at each electrode grouping (i.e., frontal, central, parietal-occipital) using permutation tests with cluster correction (Maris & Oostenveld, 2007). This is a data driven approach for identifying regions of interest in time-frequency maps, whilst maintaining alpha at .05. This approach has also been used in several past studies examining oscillatory activity during sequence learning (Heideman et al., 2018; Meissner et al., 2018). An overview of the procedure used for this study is now described.

Separate permutation tests were undertaken for the sequence learning and general motor learning contrasts and for each electrode grouping (i.e., frontal, central, parietal-occipital). Permutation testing for the sequence learning contrast involved randomizing Block 6 and Block 7 labels, at the participant level, to create $t$-maps that assumed no reliable differences in the contrast. The approach used to test the general motor learning contrast randomized Block 1 and Block 7 labels. For each contrast, a total of 100,000 permutations were undertaken. Data from permutation testing were used to define a null distribution in order to threshold non-significant individual pixels ($p < .05$, two tailed) in $t$-maps of the 'real' or non-permutated data. Clusters were then identified in these $t$-maps. A cluster was defined as two or more connected significant pixel values using MATLAB's 'bwconncomp' function. A cluster in the 'real' $t$-map was only retained if the absolute average $t$-value of the cluster, was greater than 97.5% (which corresponds to $p < .05$, two tailed) of average cluster $t$-values computed using the permutated $t$-maps.

Finally, a series of analyses examined the effect of handedness on the data. The results of these analyses are reported in the Supplementary data analysis section. Seven participants in the study were left-handed and operated the response panel with their right hand. Two sets of Supplementary analyses were undertaken examining the effects of handedness on the data. First, the correlation between performance on the SRT task and scores from the Edinburgh Handedness Inventory (Oldfield, 1971)

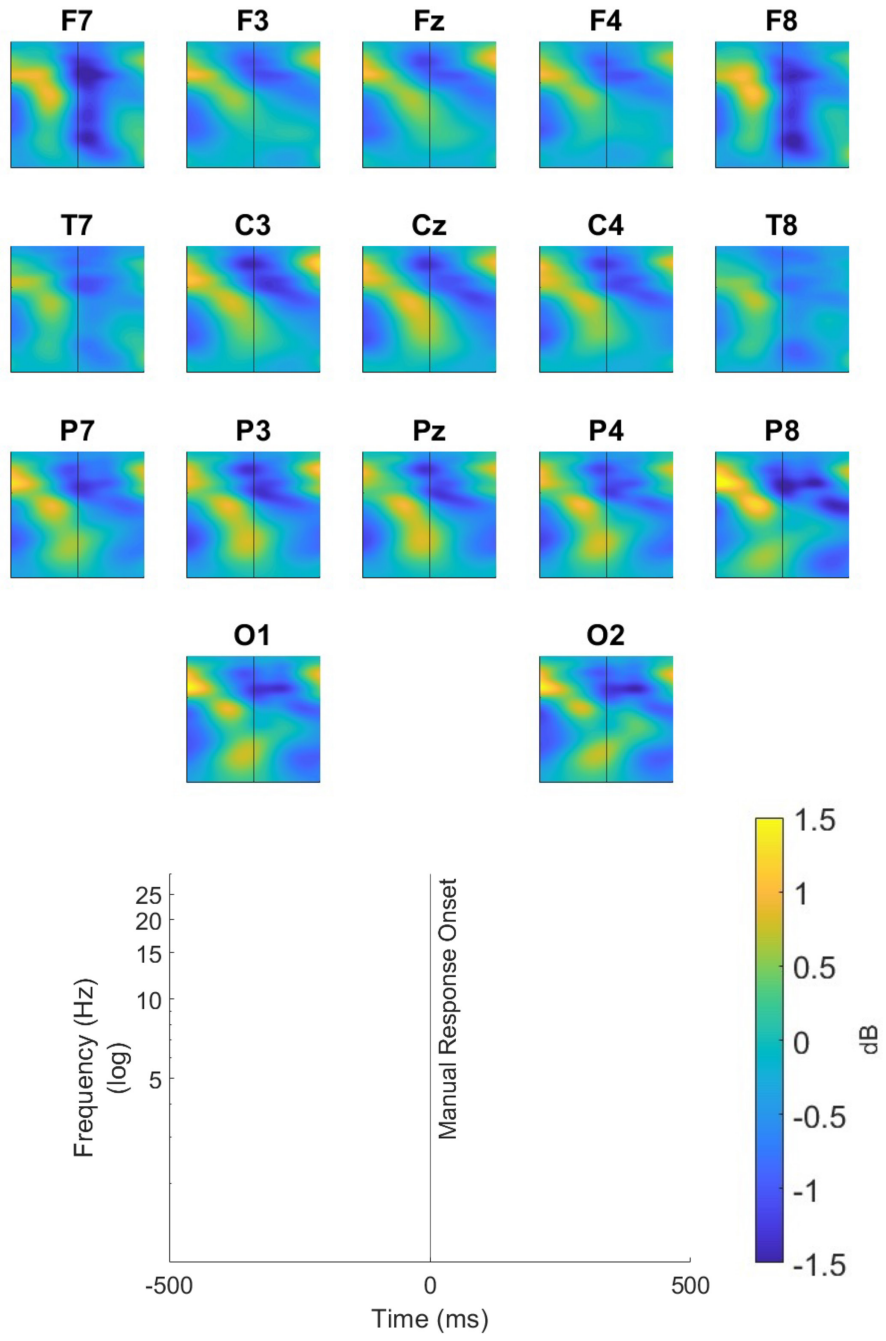


**FIGURE 2** Grand average time-frequency plots at each electrode. Yellow indicates an increase in power (dB) from baseline, and blue a decrease. The time-frequency plots show data averaged across trials, blocks and participants

were computed. No significant correlations were found. Second, time-frequency analysis and permutation testing were repeated, but only with right-handed participants. Overall, these analyses revealed that excluding left-handed participants had no effect on the current results.

## 3 | RESULTS

### 3.1 | Analyses of manual reaction times

Figure 4 presents mean reaction times reported by block. This figure shows reaction times decreased across Blocks 1–6 before increasing on Block 7. The repeated measures ANOVA revealed a significant main effect of Block on reaction times ($F$ [4.885, 238.362] = 27.225, $p < .001$, *partial* $\eta^2$ = .357). This analysis reports Greenhouse–Geisser corrected results, addressing violations in sphericity. Both the general motor learning and sequence learning contrasts were significant. Reaction times on Block 7 were significantly faster compared with Block 1 ($t$ [49] = 2.796, $p_{\text{corrected}}$ = .014, Cohen's $d$ = 0.395). Also, reaction times on Block 7 were significantly slower compared with Block 6 ($t$ [49] = 7.736, $p_{\text{corrected}} < .001$, Cohen's $d$ = 1.094).

## 3.2 | Analyses of oscillatory power

Time-Frequency plots presenting oscillatory power (in dB) presented by Electrode Grouping (i.e., Frontal, Central, Parietal-Occipital) and Block (i.e., Block 1–7) are presented in Figure 5.

The results from the permutation tests of the general motor learning and sequence learning contrasts are presented in Figures 6 and 7 respectively. Permutation testing of the general motor learning contrast is shown in Panel A of Figure 6. The analysis identified a significant cluster comprising frequencies between 7 and 13 Hz at frontal ($p < .001$), central ($p < .001$) and parietal-occipital ($p < .001$) electrode groupings. This cluster was present before a manual response was made. The direction of the *t*-values indicates power was higher on Block 7, compared with Block 1. This trend is further illustrated in Panel B of Figure 6. This panel shows the average power of the 7–13 Hz cluster, averaged across frontal, central and parietal-occipital sites, computed separately for each block. Paired sample *t*-tests with Bonferroni corrected *p*-values were used to examine general motor learning and sequence learning effects in these data. The analysis replicated the results from the permutation tests showing power increased from Block 1 to Block 7 ($t$ [49] = 5.954, $p_{corrected} < .001$, Cohen's $d = 0.842$). The sequence learning contrast was also significant for this cluster. Power increased from Block 6 to Block 7 ($t$ [49] = 2.540, $p_{corrected} = .028$, Cohen's $d = 0.359$).

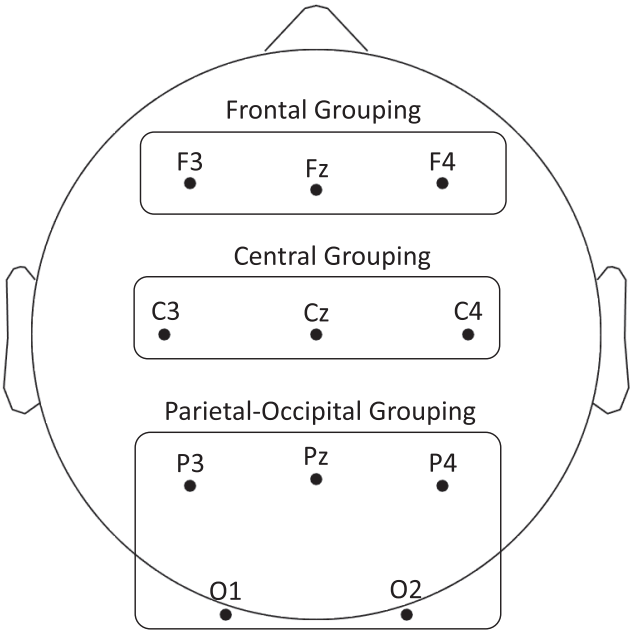


**FIGURE 3** Overview of electrode groupings. The frontal grouping comprised electrodes F3, Fz and F4. The central grouping C3, Cz and C4. The parietal-occipital grouping P3, Pz, P4, O1 and O2. Electrodes excluded from the analyses were Fp1, Fp2, F7, F8, T7, T8, P7, P8, M1 and M2 (these are not shown in the figure)

Permutation testing for the general motor contrast also revealed an additional cluster with a frequency range between 13 and 20 Hz. This cluster was only present at the parietal-occipital grouping. This cluster occurred at the time a manual response was made. For this cluster, the direction of the *t*-values indicates power was lower on Block 7, compared with Block 1. Panel C of Figure 6 shows the averaged power for this 13–20 Hz cluster, at the parietal-occipital site, computed separately for each block. This panel shows power for this cluster decreased across the SRT task. This was confirmed using paired sample *t*-tests with Bonferroni corrected *p*-values. Power for the 13–20 Hz cluster significantly decreased from Block 1 to Block 7 ($t$ [49] = 4.218, $p_{corrected} < .001$, Cohen's $d = 0.596$). The sequence learning contrast was not significant for this cluster. The difference in power between Block 6 and Block 7 was not significant ($t$ [49] = 0.115, $p_{corrected} = .999$, Cohen's $d = 0.016$).

The results of the permutation testing of the sequence learning contrast are presented in Panel A of Figure 7. The analysis identified significant clusters at frontal ($p = .021$) and central ($p = .003$) electrode groupings. The frequency

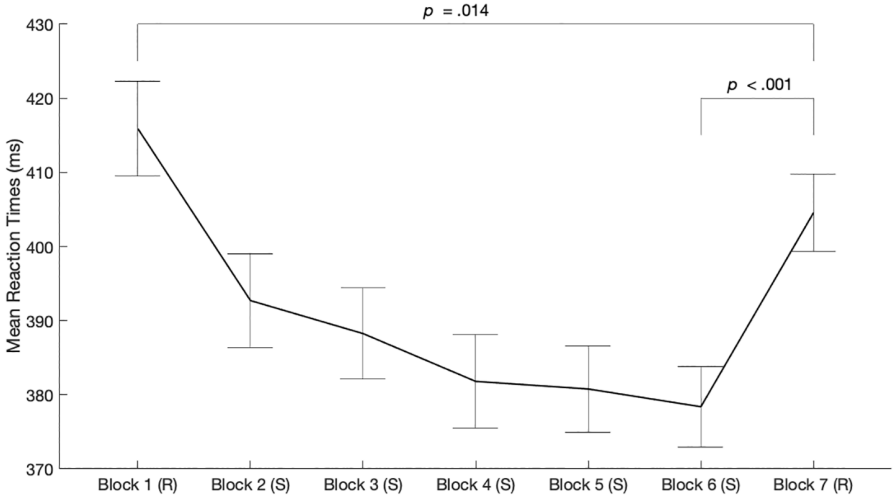


**FIGURE 4** Mean reaction times reported by block. Letter in parenthesis denotes block comprised either random trials (R) or sequence trials (S). Error bars show standard error

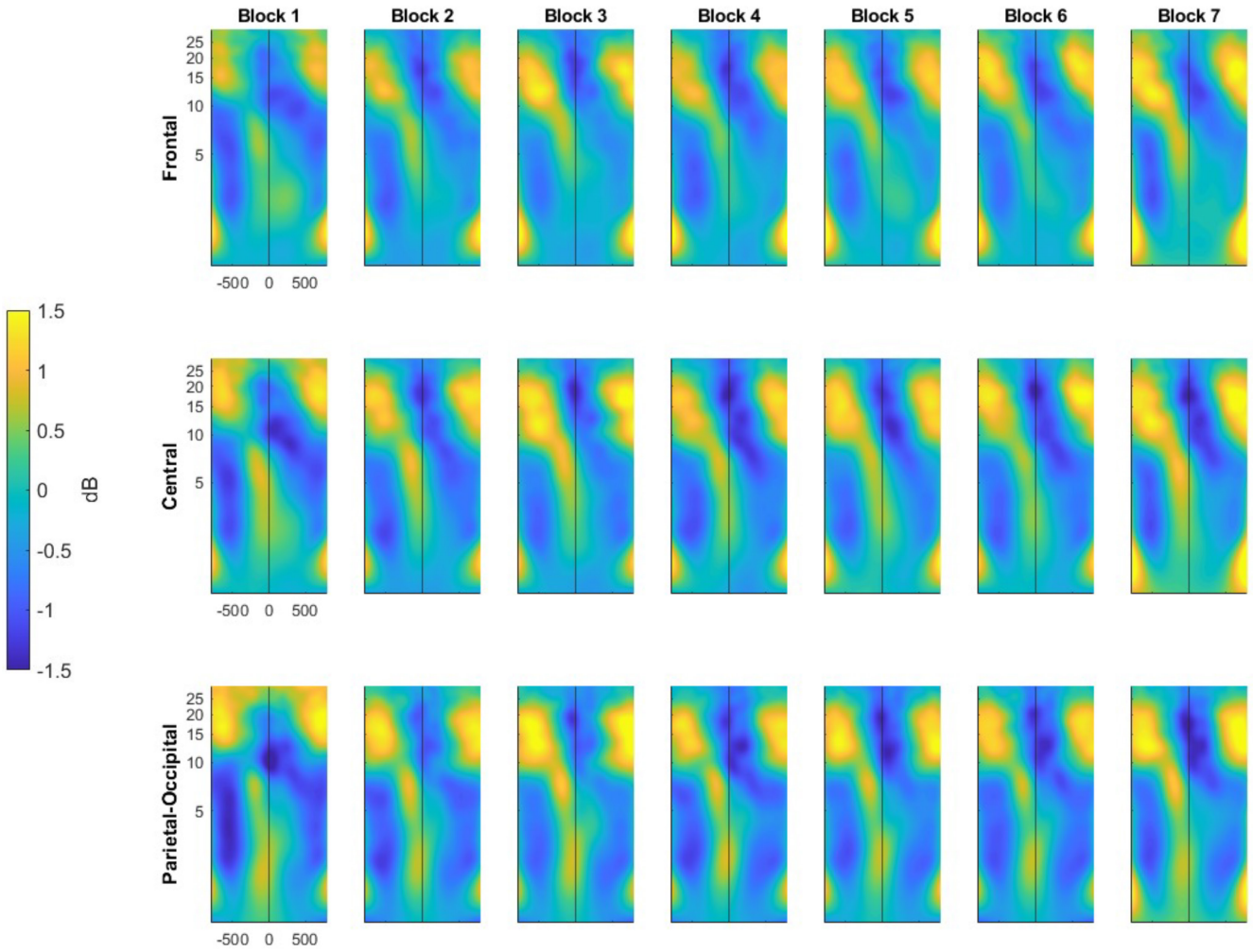


**FIGURE 5** Time-frequency plots showing change in oscillatory power from baseline (dB), reported by electrode grouping and block

range of the clusters was between approximately 4–7 Hz and mainly present before manual response onset. The direction of the *t*-values in Panel A indicate power was higher on Block 7 (random) compared to Block 6 (sequence). Panel B shows the average power associated with these clusters computed separately for each block. Paired sample *t*-tests replicated the results from the permutation tests showing sequence learning effects. This analysis found that average power of the 4–7 Hz cluster on Block 7 was significantly higher compared to Block 6 ($t$ [49] = 4.831, $p_{\text{corrected}} < .001$, Cohen's $d$ = 0.683). The general motor learning contrast (i.e., Block 1 vs. Block 7) for this cluster was not significant ($t$ [49] = 1.881, $p_{\text{corrected}} = .132$, Cohen's $d = 0.266$).

## 3.3 | Correlations between reaction times and oscillatory power

A set of exploratory analyses were undertaken to examine the relationship between the behavioral measures of learning, both general and sequence, and oscillatory power. An index of general motor learning was computed by subtracting Block 7 reaction time data from Block 1 (i.e., Block 1–Block 7). Positive values on this index indicate an increase in the speed responding to the visual stimulus at the end of the task, compared to the start. A sequence learning index was computed by subtracting Block 6 reaction times from Block 7 (i.e., Block 7–Block 6). Positive values for this index would indicate greater sensitivity to the sequence and greater levels of sequence learning. The general motor learning and sequence learning indices were also computed for the average of the 7–13 Hz (using data presented in Panel B of Figure 6), 13–20 Hz (Panel C of Figure 6) and 4–7 Hz (Panel B of Figure 7) clusters. Correlations between reaction times and oscillatory power were computed using Spearman's ρ. The general learning index, measured by reaction times, was not found to be significantly correlated with the corresponding index for the 7–13 Hz ($\rho = .010$, $p = .943$), 13–20 Hz ($\rho = .019$, $p = .864$) or 4–7 Hz ($\rho = -.005$, $p = .975$) clusters. Similarly, the sequence learning index computed using reaction times, was not found to be significantly correlated

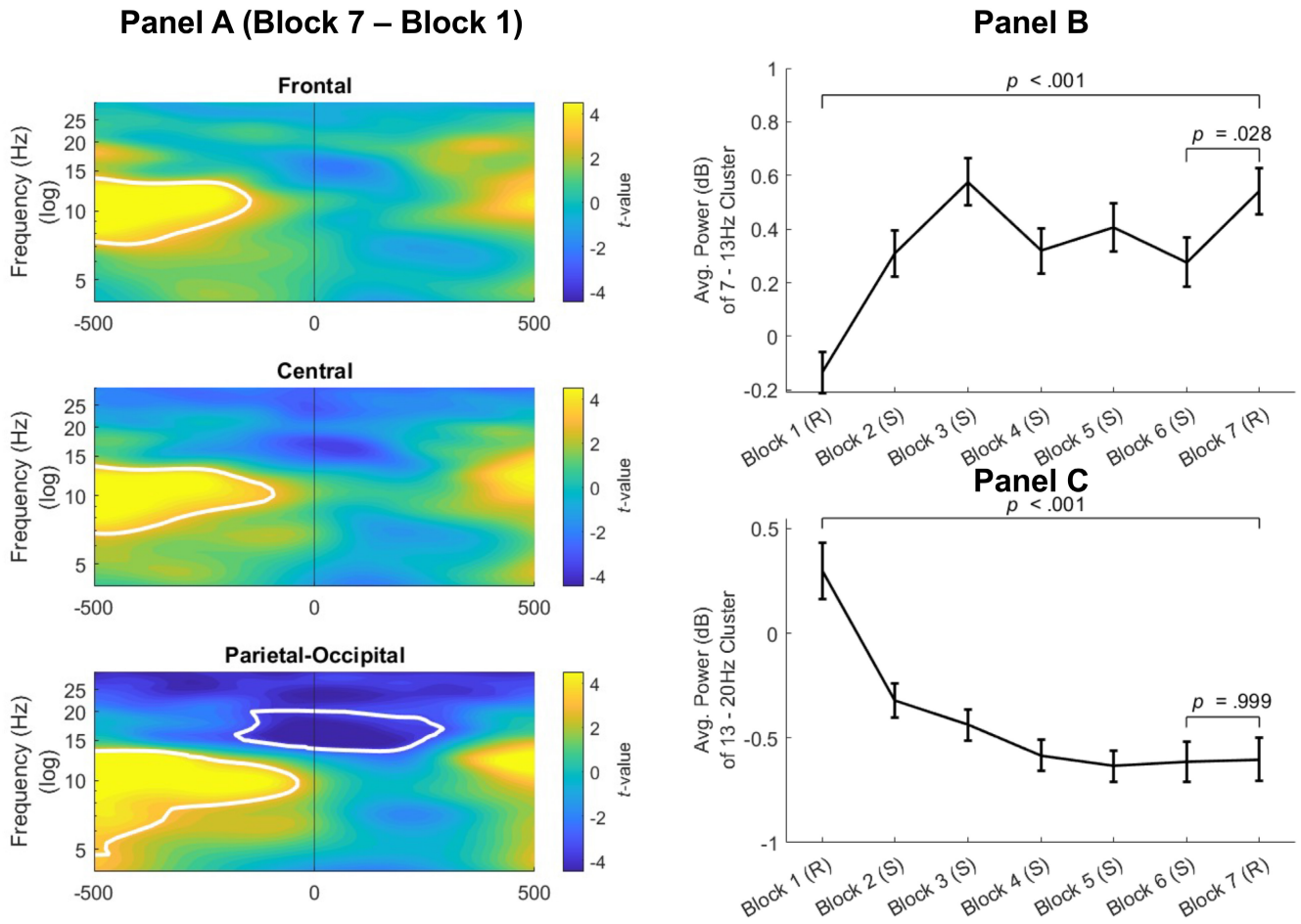


**FIGURE 6** Panel A shows time-frequency *t*-maps testing the general motor learning contrast. A manual response is made at time zero. In Panel A, the white contour shows a cluster that comprised power in the 7–13 Hz range at frontal, central and parietal-occipital electrode groupings. The direction of the *t*-values indicates power for these clusters was higher on Block 7 compared to Block 1. An additional cluster was found at the parietal-occipital grouping that comprised power in the 13–20 Hz range. Power in this frequency range was lower on Block 7 compared to Block 1. Panels B and C show the average power associated with the 7–13 Hz and 13 - 20 Hz clusters respectively, reported by block. In these panels, error bars show standard error

with the average power from the sequence learning index from the 7–13 Hz ($\rho = .156$, $p = .277$), 13–20 Hz ($\rho = -.100$, $p = .490$) or 4–7 Hz ($\rho = .108$, $p = .455$) clusters.

## 4 | DISCUSSION

This study examined changes in oscillatory power during implicit motor sequence learning. Analyses of the behavioral data indicated sequence learning and general motor learning effects were present. Consistent with earlier studies (Deroost et al., 2006; Lukács & Kemény, 2015; Lum, 2020; Lum et al., 2019; Nissen & Bullemer, 1987; Thomas et al., 2004; Thomas & Nelson, 2001), sequence learning was evident from the analysis showing reaction times increased from the final sequence block to the following random block (see Figure 4). The results of the permutation tests indicated theta was modulated by this type of learning, with power between 4–7 Hz found to be significantly lower on the final sequence block than the following random block. Permutation tests did not indicate alpha and beta modulations were associated with sequence learning. Rather, oscillatory activity in these frequency bands appears to be related to general motor learning, that is learning or executing stimulus response associations. Permutation tests revealed 7–13 Hz power increased, and 13–20 Hz power decreased from the first to last random block of trials. At the behavioral level, reaction times over these blocks became faster (see Figure 4), as seen in past research (Marcus et al., 2006). This suggests a role of alpha and beta band activity with respect to generating increasingly faster manual responses to non-predictable visual stimuli. This may occur as stimulus–response associations are established and then strengthened. Since the SRT task used in the current study only examined learning, our findings do not rule out the role of alpha and beta

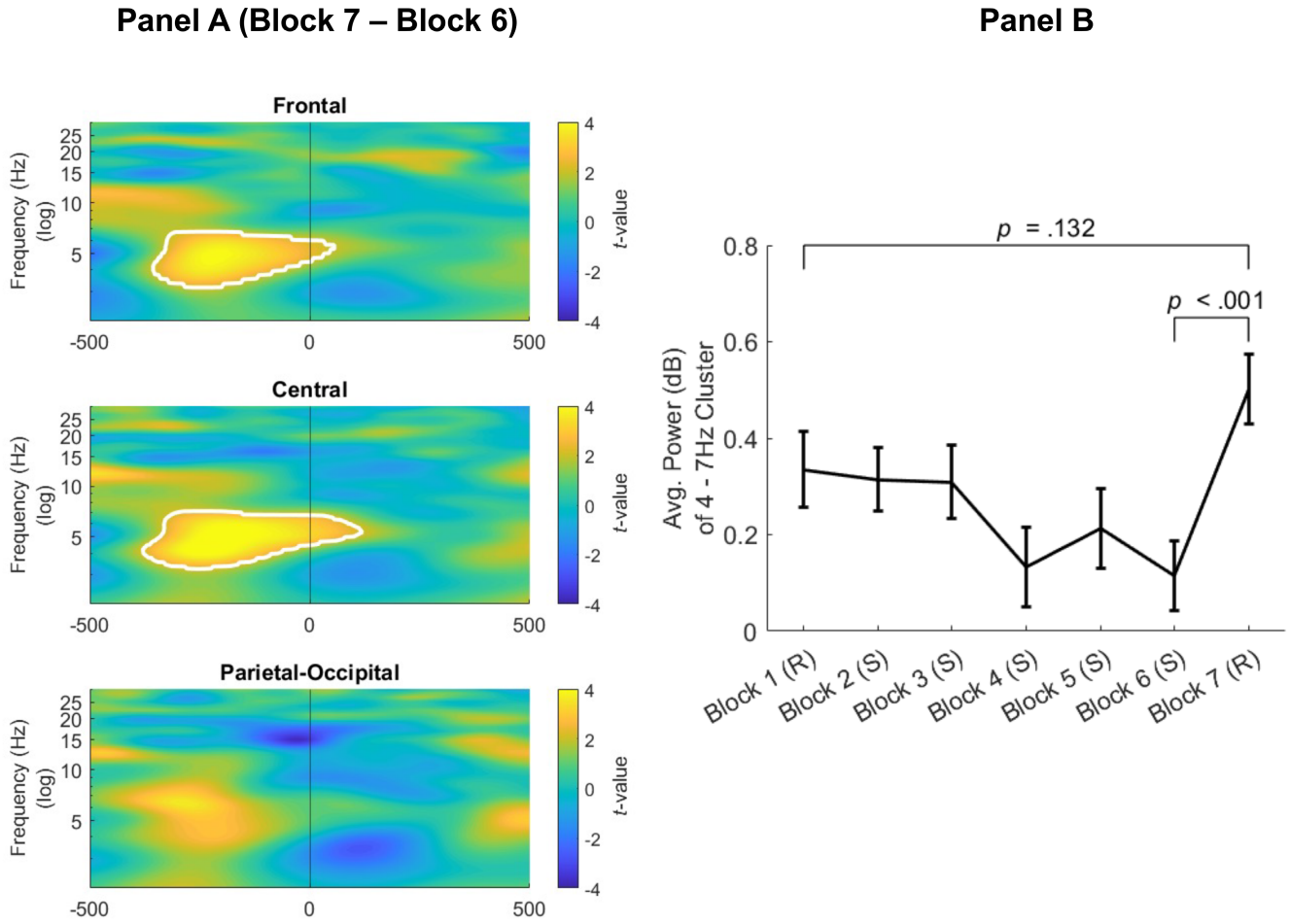


**FIGURE 7** Panel A shows time-frequency *t*-maps testing the sequence learning contrast. A manual response is made at time zero. In Panel A, the white contour shows a cluster that comprised power in the 4–7 Hz range at frontal and central electrode groupings. The direction of the *t*-values indicates power in the 4–7 Hz range was higher in Block 7 compared to Block 6. Panel B shows the average of the 4–7 Hz cluster reported by block. Error bars show standard error

oscillations in retention or consolidation processes (e.g., Pollok et al., 2014, 2015). Nevertheless, the study demonstrates for the first time, that decreases in theta power are associated with implicit motor sequence learning on the SRT task.

In healthy controls, increases in theta power occur when completing a task that places greater demands on attentional resources (Clayton et al., 2015; Sauseng et al., 2007) and temporal sequencing of information in declarative and working memory (Burke et al., 2014; Canolty et al., 2006; Herweg et al., 2020; Roux & Uhlhaas, 2014). The results of the current study may indicate that these processes are disengaged during implicit forms of learning, since theta power was lower on sequence trials compared to random. One explanation for this finding is that theta desynchronisation promotes implicit forms of sequence learning (e.g., Janacsek et al., 2012; Nemeth et al., 2013; Tóth et al., 2017). Janacsek et al. (2012) proposed implicit learning of sequences and statistical regularities may be optimized when bottom-up processing of sensory information drives the learning. Put another way, top-down influences on learning may shift attention away from the regularities present in the sensory input and disrupt the learning process. In support of this position, Tóth et al. (2017) found that implicit learning of a probabilistic sequence co-occurred with decreased functional connectivity between frontal and central brain regions in the theta band. This decrease in functional connectivity was considered to reflect attentional resources and working memory no longer playing a role during learning. This may have been the case in the current study given theta power modulations were also observed at frontal and central electrode groupings. Interestingly, the correlation between indices of sequence learning based on manual reaction times and theta power was not significant. Also, the latency range of the 4–7 Hz cluster occurred before a motor response was executed. This may reflect disengagement of top-down influences with respect to processing the visual stimulus, enabling the sequence to be discovered from the moving visual target, rather than directly influencing the speed of manual responses.

The pattern of theta modulations observed in the current study are inconsistent with the data presented by Meissner et al. (2018). In their study investigating oscillatory activity in Parkinson's disease, implicit sequence learning was associated with an increase in theta power. One analysis revealed sequence learning was correlated with increases in theta power in the group with Parkinson's disease, but not controls. When considered within the framework outlined above, elevated levels of theta power during implicit learning may represent a maladaptive response to processing patterns present in visual/motoric information. This seems likely in Parkinson's disease given implicit motor sequence learning impairments are common in this disorder (Clark et al., 2014), along with atypical theta oscillatory activity (Geraedts et al., 2018). It will be interesting to test whether elevated theta levels are present on the SRT task in other disorders (e.g., Clark & Lum, 2017) who also exhibit implicit sequence learning impairments.

It is equally plausible, however, that the increase in theta power from sequence to random blocks occurred as a consequence of sequence learning. Frontal-central theta power is modulated by the attentional demands associated with processing and responding to sensory information (Clayton et al., 2015). These types of modulations also occur when differences in sensory information can be detected. For example, frontal-central theta power increases when participants detect infrequently occurring auditory or visual stimuli (Cacace & McFarland, 2003; Mazaheri & Picton, 2005). In the context of the SRT task, participants may notice slower manual responses on the random block (Rünger & Frensch, 2008), relative to the preceding sequence block, which in turn leads to an increase in theta power. From this perspective, the theta modulations observed in this study may be an outcome of sequence learning. This interpretation may also explain the absence of a significant correlation between manual reaction times and theta power. To further clarify the role of frontal-central theta oscillations during implicit motor sequence learning, non-invasive brain stimulation could be used. There is evidence to suggest frontal theta power can be manipulated using transcranial electrical stimulation or transcranial magnetic stimulation (e.g., Chander et al., 2016; Desforges et al., 2022). If theta oscillatory activity is instrumental in supporting implicit sequence learning, attenuating and/or enhancing power in this frequency band should therefore promote or disrupt performance on the SRT task.

Theta oscillations may also reflect the attentional demands associated with general motor learning, in addition to sequence learning. Tzvi et al. (2016) found theta power decreased on the SRT task, irrespective of whether participants were responding to sequence or random trials. This result was only observed at parietal electrodes, but also noted to have been likely present at unanalysed occipital electrodes as well. This finding was interpreted to suggest a decline in the attentional demands associated with providing a manual response to a visual target, that likely occurred as stimulus–response associations were established via repetition. This result was not observed in the current study. Permutation testing of the general motor learning contrast did not reveal theta power modulations. Also, theta power increased from the final sequence to following random block at frontal and central electrode sites. Differences in the analysis of the EEG data may explain these inconsistent findings and reveal distinct theta related processes during learning. Notably, Tzvi et al. (2016) averaged power over a 5-second window. This approach may be ideal for detecting overall changes in oscillatory power, that are the sum of all cognitive and motor processes associated with completing the SRT task. In contrast, time-frequency decomposition, which was used in this study and elsewhere (e.g., Heideman et al., 2018; Meissner et al., 2018), is better suited for detecting changes in oscillatory power associated with a specific event, such as executing a motor response or processing a visual stimulus. Thus, the literature may be indicating theta oscillations do not serve a singular function during implicit motor sequence learning. Rather, theta activity from distinct sources may independently support relatively micro level (e.g., executing a manual response/visual stimulus processing) and macro level processes (e.g., completing the SRT task). This possibility can be investigated in future research using high density electrode M/EEG recordings that permit distinct sources of theta power in the brain to be identified (e.g., Beese et al., 2017).

The results of this study also shed new light on the function of alpha and beta oscillations during implicit sequence learning. Permutation testing did not reveal sequence learning effects in the alpha or beta bands. Oscillatory activity in both frequency bands, however, was found to be related to general motor learning. First, permutation testing revealed an increase in alpha power (7–13 Hz) from the first to last random block. When completing visual-motor tasks, increases in alpha power reflect a decrease in levels of cortical activity associated with processing visual information and/or executing a manual response (Pfurtscheller, 1992; Pfurtscheller & Da Silva, 1999). Thus, it seems that the cortical resources needed to process a non-predictable visual target and/or execute a motor response decreased with practice, irrespective of whether a sequence was present. This likely explains the result of a *t*-test demonstrating 7–13 Hz power was significantly higher on the final random (Block 7) block, compared with the first random block (Block 1) (see Panel B of Figure 6). Learning stimulus–response

associations is one factor that likely facilitated this outcome, since activity in this frequency band was not found by the permutation test of sequence learning effects.

Second, beta power (13–20 Hz) declined from the first to final random block. Decreases in beta power or beta desynchronisation, appear to support cortical reorganization associated with motor learning (Engel & Fries, 2010). The results obtained in the current study suggest this was related to stimulus–response learning, rather than sequence learning. Indeed, in the current study, beta power decreased across the SRT task and was not sensitive to sequence learning effects (see Panel C of Figure 6). This result is not without precedent. Pollok et al. (2014) also found no significant differences in beta power between random and sequence trials on the SRT task. Also, van der Cruijsen et al. (2021) found beta power was not associated with explicit motor sequence learning, after controlling for oscillatory activity related to generating a manual response. These findings might be indicating beta oscillations play no direct role in sequence learning, beyond supporting movement (Pfurtscheller & Da Silva, 1999), for example, pressing a button on a response panel. This interpretation may explain the non-significant correlations between beta power and the manual reaction time indices of learning, observed in the current study.

Beta oscillations, however, may be needed for the long-term storage or retention of an implicitly learnt motor sequence. Pollok et al. (2014) found beta power correlated with a measure of sequence retention presented 15-minutes after the initial learning. Also, the beta power modulations on the SRT task observed by Heideman et al. (2018) may be more closely related to retention than learning. In that study, significant differences in beta power were observed between sequence and random trials, using an SRT task that comprised 864 sequence trials and administered over 45 minutes. As a comparison, the SRT task used in the current study comprised 300 sequence trials and was completed in around 10 minutes.

Beta oscillations may be specifically involved in stabilizing motor sequence knowledge, after learning has occurred. Pollok et al. (2015) administered transcranial alternating current stimulation over the primary motor cortex as participants completed the SRT task. The frequency of the alternating current used in that study aimed to increase beta or alpha oscillatory power (e.g., Berger et al., 2018). Following alpha and sham/placebo stimulation, the ability to execute the motor sequence was poorer after an interference block of trials was presented. The interference block, however, had no effect on executing the motor sequence following beta stimulation.

Finally, an important limitation associated with this research is the extent theta power modulations reflect implicit learning. In the current study, sequence awareness was assessed by asking participants if they detected a sequence or pattern in the location of the visual stimuli after they completed the SRT task. A weakness with this approach, however, is that awareness of the sequence is probed after the random block of trials has been presented (Eimer et al., 1996). As a consequence, participants who do not indicate that a sequence was present, may be responding to the random, rather than sequence block. In response to this problem, several learning paradigms have been developed that aim to quantify the effects of implicit (or unconscious) and explicit (conscious) influences on learning and memory (Jacoby, 1991). This approach has been extended to study sequence learning (Jiménez et al., 1996). It will be important for future studies to use this methodology to better understand the oscillatory dynamics associated with implicit and explicit forms of learning.

## 5 | CONCLUSION

The main finding to emerge from our study was that sequence learning related power modulations were observed in the theta band, but not alpha or beta. During implicit sequence learning theta desynchronisation may indicate disengagement of top-down influences on sensory processing, that promotes learning. Alternatively, theta power modulations may be an outcome of sequence learning. Specifically, changes in this frequency band may reflect the sensitivity of the sensory system to the presence or absence of a sequence. The study findings have implications for our understanding of the biological basis of implicit motor sequence learning deficits in a range of neurodevelopmental, neurodegenerative and psychiatric disorders who typically perform poorly on the SRT task (Clark & Lum, 2017). For example, studying theta power in these groups may reveal an electrophysiological correlate of implicit sequence learning impairments. Based on the results of the current study, elevated levels of theta power on the SRT task may be associated with suboptimal learning. Along with past research, the current study advances our understanding of the relationship between cortical oscillations and motor learning, which will be important to elucidate the neural processes underpinning skill acquisition in healthy and disordered populations.

### AUTHOR CONTRIBUTIONS

**Jarrad A. G. Lum:** Conceptualization; data curation; formal analysis; investigation; methodology; resources; software; writing – original draft; writing – review and editing. **Gillian M. Clark:** Investigation; methodology; writing – review and editing. **Pamela Barhoun:** Writing

– review and editing. **Aron T. Hill:** Writing – review and editing. **Christian Hyde:** Writing – review and editing. **Peter H. Wilson:** Writing – review and editing.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

## ACKNOWLEDGMENT

Open access publishing facilitated by Deakin University, as part of the Wiley - Deakin University agreement via the Council of Australian University Librarians.

## ORCID

*Jarrad A. G. Lum* https://orcid.org/0000-0003-2098-2403
*Pamela Barhoun* https://orcid.org/0000-0001-7238-4216

## REFERENCES

Albouy, G., Sterpenich, V., Balteau, E., Vandewalle, G., Desseilles, M., Dang-Vu, T., Darsaud, A., Ruby, P., Luppi, P. H., Degueldre, C., Peigneux, P., Luxen, A., & Maquet, P. (2008). Both the hippocampus and striatum are involved in consolidation of motor sequence memory. *Neuron*, *58*(2), 261–272. https://doi.org/10.1016/j.neuron.2008.02.008

Başar, E., Başar-Eroglu, C., Karakaş, S., & Schürmann, M. (2001). Gamma, alpha, delta, and theta oscillations govern cognitive processes. *International Journal of Psychophysiology*, *39*(2–3), 241–248. https://doi.org/10.1016/S0167-8760(00)00145-8

Beese, C., Meyer, L., Vassileiou, B., & Friederici, A. D. (2017). Temporally and spatially distinct theta oscillations dissociate a language-specific from a domain-general processing mechanism across the age trajectory. *Scientific Reports*, *7*(1), 1–11. https://doi.org/10.1038/s41598-017-11632-z

Berger, A., Pixa, N. H., Steinberg, F., & Doppelmayr, M. (2018). Brain oscillatory and hemodynamic activity in a bimanual coordination task following transcranial alternating current stimulation (tACS): A combined EEG-fNIRS study. *Frontiers in Behavioral Neuroscience*, *12*, 67. https://doi.org/10.3389/fnbeh.2018.00067

Burke, J. F., Sharan, A. D., Sperling, M. R., Ramayya, A. G., Evans, J. J., Healey, M. K., Beck, E. N., Davis, K. A., Lucas, T. H., & Kahana, M. J. (2014). Theta and high-frequency activity mark spontaneous recall of episodic memories. *Journal of Neuroscience*, *34*(34), 11355–11365. https://doi.org/10.1523/JNEUROSCI.2654-13.2014

Buzsáki, G., Logothetis, N., & Singer, W. (2013). Scaling brain size, keeping timing: Evolutionary preservation of brain rhythms. *Neuron*, *80*(3), 751–764. https://doi.org/10.1016/j.neuron.2013.10.002

Cacace, A. T., & McFarland, D. J. (2003). Spectral dynamics of electroencephalographic activity during auditory information processing. *Hearing Research*, *176*(1–2), 25–41. https://doi.org/10.1016/S0378-5955(02)00715-3

Canolty, R. T., Edwards, E., Dalal, S. S., Soltani, M., Nagarajan, S. S., Kirsch, H. E., Berger, M. S., Barbaro, N. M., & Knight, R. T. (2006). High gamma power is phase-locked to theta oscillations in human neocortex. *Science*, *313*(5793), 1626–1628. https://doi.org/10.1126/science.1128115

Chander, B. S., Witkowski, M., Braun, C., Robinson, S. E., Born, J., Cohen, L. G., Birbaumer, N., & Soekadar, S. R. (2016). tACS phase locking of frontal midline theta oscillations disrupts working memory performance. *Frontiers in Cellular Neuroscience*, *10*, 120. https://doi.org/10.3389/fncel.2016.00120

Clark, G. M., & Lum, J. A. (2017). Procedural learning in Parkinson's disease, specific language impairment, dyslexia, schizophrenia, developmental coordination disorder, and autism spectrum disorders: A second-order meta-analysis. *Brain and Cognition*, *117*, 41–48. https://doi.org/10.1016/j.bandc.2017.07.004

Clark, G. M., Lum, J. A., & Ullman, M. T. (2014). A meta-analysis and meta-regression of serial reaction time task performance in Parkinson's disease. *Neuropsychology*, *28*(6), 945–958.

Clayton, M. S., Yeung, N., & Kadosh, R. C. (2015). The roles of cortical oscillations in sustained attention. *Trends in Cognitive Sciences*, *19*(4), 188–195. https://doi.org/10.1016/j.tics.2015.02.004

Cleeremans, A., Destrebecqz, A., & Boyer, M. (1998). Implicit learning: News from the front. *Trends in Cognitive Sciences*, *2*(10), 406–416. https://doi.org/10.1016/S1364-6613(98)01232-7

Clegg, B. A., DiGirolamo, G. J., & Keele, S. W. (1998). Sequence learning. *Trends in Cognitive Sciences*, *2*(8), 275–281. https://doi.org/10.1016/S1364-6613(98)01202-9

Cohen, J. (2013). *Statistical power analysis for the behavioral sciences* (2nd ed.). Routledge.

Cohen, M. X. (2014). *Analyzing neural time series data: Theory and practice*. MIT press.

Cohen, M. X., Cavanagh, J. F., & Slagter, H. A. (2011). Event-related potential activity in the basal ganglia differentiates rewards from nonrewards: Temporospatial principal components analysis and source localization of the feedback negativity: Commentary. *Human Brain Mapping*, *32*(12), 2270–2271. https://doi.org/10.1002/hbm.21358

Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*(1), 9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009

Deroost, N., Zeeuws, I., & Soetens, E. (2006). Effector-dependent and response location learning of probabilistic sequences in serial reaction time tasks. *Experimental Brain Research*, *171*(4), 469–480. https://doi.org/10.1007/s00221-005-0294-5

Desforges, M., Hadas, I., Mihov, B., Morin, Y., Rochette Braün, M., Lioumis, P., Zomorrodi, R., Théoret, H., Lepage, M., Daskalakis, Z. J., & Tremblay, S. (2022). Dose-response of intermittent theta burst stimulation of the prefrontal cortex: A TMS-EEG study. *Clinical Neurophysiology*, *136*, 158–172. https://doi.org/10.1016/j.clinph.2021.12.018

Eimer, M., Goschke, T., Schlaghecken, F., & Stürmer, B. (1996). Explicit and implicit learning of event sequences: Evidence from event-related brain potentials. *Journal of Experimental*

*Psychology: Learning, Memory, and Cognition*, *22*(4), 970–987. https://doi.org/10.1037/0278-7393.22.4.970

Engel, A. K., & Fries, P. (2010). Beta-band oscillations—Signalling the status quo? *Current Opinion in Neurobiology*, *20*(2), 156–165. https://doi.org/10.1016/j.conb.2010.02.015

Fiser, J., & Aslin, R. N. (2002). Statistical learning of higher-order temporal structure from visual shape sequences. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *28*(3), 458–467. https://doi.org/10.1037/0278-7393.28.3.458

Geraedts, V. J., Boon, L. I., Marinus, J., Gouw, A. A., van Hilten, J. J., Stam, C. J., Tannemaat, M. R., & Contarino, M. F. (2018). Clinical correlates of quantitative EEG in Parkinson disease: A systematic review. *Neurology*, *91*(19), 871–883. https://doi.org/10.1212/WNL.0000000000006473

Hamrick, P., Lum, J. A. G., & Ullman, M. T. (2018). Child first language and adult second language are both tied to general-purpose learning systems. *Proceedings of the National Academy of Sciences*, *115*(7), 1487–1492. https://doi.org/10.1073/pnas.1713975115

Hardwick, R. M., Rottschy, C., Miall, R. C., & Eickhoff, S. B. (2013). A quantitative meta-analysis and review of motor learning in the human brain. *NeuroImage*, *67*, 283–297. https://doi.org/10.1016/j.neuroimage.2012.11.020

Heideman, S. G., van Ede, F., & Nobre, A. C. (2018). Temporal alignment of anticipatory motor cortical beta lateralisation in hidden visual-motor sequences. *European Journal of Neuroscience*, *48*(8), 2684–2695. https://doi.org/10.1111/ejn.13700

Herweg, N. A., Solomon, E. A., & Kahana, M. J. (2020). Theta oscillations in human memory. *Trends in Cognitive Sciences*, *24*(3), 208–227. https://doi.org/10.1016/j.tics.2019.12.006

Isbilen, E. S., McCauley, S. M., Kidd, E., & Christiansen, M. H. (2020). Statistically induced chunking recall: A memory-based approach to statistical learning. *Cognitive Science*, *44*(7), e12848. https://doi.org/10.1111/cogs.12848

Jackson, A. F., & Bolger, D. J. (2014). The neurophysiological bases of EEG and EEG measurement: A review for the rest of us. *Psychophysiology*, *51*(11), 1061–1071. https://doi.org/10.1111/psyp.12283

Jacoby, L. L. (1991). A process dissociation framework: Separating automatic from intentional uses of memory. *Journal of Memory and Language*, *30*(5), 513–541. https://doi.org/10.1016/0749-596X(91)90025-F

Janacsek, K., Fiser, J., & Nemeth, D. (2012). The best time to acquire new skills: Age-related differences in implicit sequence learning across the human lifespan. *Developmental Science*, *15*(4), 496–505. https://doi.org/10.1111/j.1467-7687.2012.01150.x

Janacsek, K., & Nemeth, D. (2013). Implicit sequence learning and working memory: Correlated or complicated? *Cortex*, *49*(8), 2001–2006. https://doi.org/10.1016/j.cortex.2013.02.012

Janacsek, K., Shattuck, K. F., Tagarelli, K. M., Lum, J. A., Turkeltaub, P. E., & Ullman, M. T. (2020). Sequence learning in the human brain: A functional neuroanatomical meta-analysis of serial reaction time studies. *NeuroImage*, *207*, 116387. https://doi.org/10.1016/j.neuroimage.2019.116387

Jiménez, L., Mendez, C., & Cleeremans, A. (1996). Comparing direct and indirect measures of sequence learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *22*(4), 948–969. https://doi.org/10.1037/0278-7393.22.4.948

Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: The inhibition–timing hypothesis. *Brain Research Reviews*, *53*(1), 63–88. https://doi.org/10.1016/j.brainresrev.2006.06.003

Koch, F.-S., Sundqvist, A., Thornberg, U. B., Nyberg, S., Lum, J. A., Ullman, M. T., Barr, R., Rudner, M., & Heimann, M. (2020). Procedural memory in infancy: Evidence from implicit sequence learning in an eye-tracking paradigm. *Journal of Experimental Child Psychology*, *191*, 104733. https://doi.org/10.1016/j.jecp.2019.104733

Lewicki, P., Hill, T., & Bizot, E. (1988). Acquisition of procedural knowledge about a pattern of stimuli that cannot be articulated. *Cognitive Psychology*, *20*(1), 24–37. https://doi.org/10.1016/0010-0285(88)90023-0

Lukács, Á., & Kemény, F. (2015). Development of different forms of skill learning throughout the lifespan. *Cognitive Science*, *39*(2), 383–404. https://doi.org/10.1111/cogs.12143

Lum, J. A. G. (2020). Incidental learning of a visuo-motor sequence modulates saccadic amplitude: Evidence from the serial reaction time task. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *46*(10), 1881–1891. https://doi.org/10.1037/xlm0000917

Lum, J. A. G., Lammertink, I., Clark, G. M., Fuelscher, I., Hyde, C., Enticott, P. G., & Ullman, M. T. (2019). Visuospatial sequence learning on the serial reaction time task modulates the P1 event-related potential. *Psychophysiology*, *56*(2), e13292. https://doi.org/10.1111/psyp.13292

Marcus, D. J., Karatekin, C., & Markiewicz, S. (2006). Oculomotor evidence of sequence learning on the serial reaction time task. *Memory & Cognition*, *34*(2), 420–432. https://doi.org/10.3758/BF03193419

Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG-and MEG-data. *Journal of Neuroscience Methods*, *164*(1), 177–190. https://doi.org/10.1016/j.jneumeth.2007.03.024

Mazaheri, A., & Picton, T. W. (2005). EEG spectral dynamics during discrimination of auditory and visual targets. *Cognitive Brain Research*, *24*(1), 81–96. https://doi.org/10.1016/j.cogbrainres.2004.12.013

Meissner, S. N., Krause, V., Südmeyer, M., Hartmann, C. J., & Pollok, B. (2018). The significance of brain oscillations in motor sequence learning: Insights from Parkinson's disease. *NeuroImage: Clinical*, *20*, 448–457. https://doi.org/10.1016/j.nicl.2018.08.009

Meissner, S. N., Krause, V., Südmeyer, M., Hartmann, C. J., & Pollok, B. (2019). Pre-stimulus beta power modulation during motor sequence learning is reduced in'Parkinson's disease. *NeuroImage: Clinical*, *24*, 102057. https://doi.org/10.1016/j.nicl.2019.102057

Mognon, A., Jovicich, J., Bruzzone, L., & Buiatti, M. (2011). ADJUST: An automatic EEG artifact detector based on the joint use of spatial and temporal features. *Psychophysiology*, *48*(2), 229–240. https://doi.org/10.1111/j.1469-8986.2010.01061.x

Nemeth, D., Janacsek, K., Polner, B., & Kovacs, Z. A. (2013). Boosting human learning by hypnosis. *Cerebral Cortex*, *23*(4), 801–805. https://doi.org/10.1093/cercor/bhs068

Nissen, M. J., & Bullemer, P. (1987). Attentional requirements of learning: Evidence from performance measures. *Cognitive Psychology*, *19*(1), 1–32. https://doi.org/10.1016/0010-0285(87)90002-8

Nunez, P. L., & Srinivasan, R. (2006). *Electric fields of the brain: The neurophysics of EEG*. Oxford University Press.

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*(1), 97–113. https://doi.org/10.1016/0028-3932(71)90067-4

Pascual-Leone, A., Wassermann, E. M., Grafman, J., & Hallett, M. (1996). The role of the dorsolateral prefrontal cortex in implicit procedural learning. *Experimental Brain Research*, *107*(3), 479–485. https://doi.org/10.1007/BF00230427

Pfurtscheller, G. (1992). Event-related synchronization (ERS): An electrophysiological correlate of cortical areas at rest. *Electroencephalography and Clinical Neurophysiology*, *83*(1), 62–69. https://doi.org/10.1016/0013-4694(92)90133-3

Pfurtscheller, G. (2001). Functional brain imaging based on ERD/ERS. *Vision Research*, *41*(10–11), 1257–1260. https://doi.org/10.1016/S0042-6989(00)00235-2

Pfurtscheller, G., & Da Silva, F. L. (1999). Event-related EEG/MEG synchronization and desynchronization: Basic principles. *Clinical Neurophysiology*, *110*(11), 1842–1857. https://doi.org/10.1016/S1388-2457(99)00141-8

Poldrack, R. A., & Rodriguez, P. (2003). Sequence learning: what's the hippocampus to do? *Neuron*, *37*(6), 891–893. https://doi.org/10.1016/S0896-6273(03)00159-4

Pollok, B., Boysen, A.-C., & Krause, V. (2015). The effect of transcranial alternating current stimulation (tACS) at alpha and beta frequency on motor learning. *Behavioural Brain Research*, *293*, 234–240. https://doi.org/10.1016/j.bbr.2015.07.049

Pollok, B., Latz, D., Krause, V., Butz, M., & Schnitzler, A. (2014). Changes of motor-cortical oscillations associated with motor learning. *Neuroscience*, *275*, 47–53. https://doi.org/10.1016/j.neuroscience.2014.06.008

Robertson, E. M. (2007). The serial reaction time task: Implicit motor skill learning? *Journal of Neuroscience*, *27*(38), 10073–10075. https://doi.org/10.1523/JNEUROSCI.2747-07.2007

Roux, F., & Uhlhaas, P. J. (2014). Working memory and neural oscillations: Alpha–gamma versus theta–gamma codes for distinct WM information? *Trends in Cognitive Sciences*, *18*(1), 16–25. https://doi.org/10.1016/j.tics.2013.10.010

Rozengurt, R., Barnea, A., Uchida, S., & Levy, D. A. (2016). Theta EEG neurofeedback benefits early consolidation of motor sequence learning. *Psychophysiology*, *53*(7), 965–973. https://doi.org/10.1111/psyp.12656

Rünger, D., & Frensch, P. A. (2008). How incidental sequence learning creates reportable knowledge: The role of unexpected events. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *34*(5), 1011–1026. https://doi.org/10.1037/a0012942

Saffran, J. R., Newport, E. L., Aslin, R. N., Tunick, R. A., & Barrueco, S. (1997). Incidental language learning: Listening (and learning) out of the corner of your ear. *Psychological Science*, *8*(2), 101–105. https://doi.org/10.1111/j.1467-9280.1997.tb00690.x

Sauseng, P., Hoppe, J., Klimesch, W., Gerloff, C., & Hummel, F. C. (2007). Dissociation of sustained attention from central executive functions: Local activity and interregional connectivity in the theta range. *European Journal of Neuroscience*, *25*(2), 587–593. https://doi.org/10.1111/j.1460-9568.2006.05286.x

Schendan, H. E., Searl, M. M., Melrose, R. J., & Stern, C. E. (2003). An fMRI study of the role of the medial temporal lobe in implicit and explicit sequence learning. *Neuron*, *37*(6), 1013–1025. https://doi.org/10.1016/S0896-6273(03)00123-5

Thomas, K. M., Hunt, R. H., Vizueta, N., Sommer, T., Durston, S., Yang, Y., & Worden, M. S. (2004). Evidence of developmental differences in implicit sequence learning: An fMRI study of children and adults. *Journal of Cognitive Neuroscience*, *16*(8), 1339–1351. https://doi.org/10.1162/0898929042304688

Thomas, K. M., & Nelson, C. A. (2001). Serial reaction time learning in preschool-and school-age children. *Journal of Experimental Child Psychology*, *79*(4), 364–387. https://doi.org/10.1006/jecp.2000.2613

Tóth, B., Janacsek, K., Takács, Á., Kóbor, A., Zavecz, Z., & Nemeth, D. (2017). Dynamics of EEG functional connectivity during statistical learning. *Neurobiology of Learning and Memory*, *144*, 216–229. https://doi.org/10.1016/j.nlm.2017.07.015

Tzvi, E., Verleger, R., Münte, T. F., & Krämer, U. M. (2016). Reduced alpha-gamma phase amplitude coupling over right parietal cortex is associated with implicit visuomotor sequence learning. *NeuroImage*, *141*, 60–70. https://doi.org/10.1016/j.neuroimage.2016.07.019

van der Cruijsen, J., Manoochehri, M., Jonker, Z. D., Andrinopoulou, E.-R., Frens, M. A., Ribbers, G. M., Schouten, A. C., & Selles, R. W. (2021). Theta but not beta power is positively associated with better explicit motor task learning. *NeuroImage*, *240*, 118373. https://doi.org/10.1016/j.neuroimage.2021.118373

Ward, L. M. (2003). Synchronous neural oscillations and cognitive processes. *Trends in Cognitive Sciences*, *7*(12), 553–559. https://doi.org/10.1016/j.tics.2003.10.012

World Medical Association. (2001). World medical association declaration of Helsinki. Ethical principles for medical research involving human subjects. *Bulletin of the World Health Organization*, *79*(4), 373.

Zhuang, P., Toro, C., Grafman, J., Manganotti, P., Leocani, L., & Hallett, M. (1997). Event-related desynchronization (ERD) in the alpha frequency during development of implicit and explicit learning. *Electroencephalography and Clinical Neurophysiology*, *102*(4), 374–381. https://doi.org/10.1016/S0013-4694(96)96030-7

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**How to cite this article:** Lum, J. A. G., Clark, G. M., Barhoun, P., Hill, A. T., Hyde, C., & Wilson, P. H. (2023). Neural basis of implicit motor sequence learning: Modulation of cortical power. *Psychophysiology*, *60*, e14179. https://doi.org/10.1111/psyp.14179