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Flexible modulation of premotor mu rhythm waveform shape predicts human motor sequence learning

<https://doi.org/10.1523/JNEUROSCI.0198-26.2026>

Received: 30 January 2026

Revised: 21 August 2026

Accepted: 29 August 2026

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This Early Release article has been peer reviewed and accepted, but has not been through the composition and copyediting processes. The final version may differ slightly in style or formatting and will contain links to any extended data.

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Title: Flexible modulation of premotor mu rhythm waveform shape predicts human motor sequence learning

Abbreviated title: Motor learning & premotor mu peak-trough symmetry

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Number of words

Abstract: 249

Significance statement: 120

Introduction: 780

Discussion: 1800

Conflicts of interest: The authors declare no conflicts of interest.

Abstract

Motor sequence learning recruits a distributed sensorimotor network. Within this network, the premotor cortex (PMC) encodes and represents sequence information while the primary motor cortex (M1) executes movement sequences. Like M1, PMC neuronal populations exhibit mu (8-13 Hz) rhythms, which are typically non-sinusoidal. Previous studies showed that mu rhythm phase gates corticospinal transmission, sensitivity to LTP-like plasticity, and learning-related corticospinal plasticity. However, these studies treated mu peak and trough phases as discrete functional states and focused exclusively on M1. Here, we characterized mu phase-dependent mechanisms of motor sequence learning by measuring waveform shape, which is a more holistic measure that treats peak and trough phases as continuous components of the same oscillatory cycle. Using cycle-by-cycle analysis of resting EEG, we quantified the peak-trough symmetry of mu rhythms recorded over premotor regions during, before, and after healthy adults (25 females, 11 males) practiced a serial reaction time task (SRTT) containing a repeating, embedded sequence (sequence group) or no sequence (no-sequence group). As learning progressed, premotor mu rhythms became more symmetric in the sequence than the no-sequence group; these symmetry increases were also more positively correlated with skill acquisition in the sequence than the no-sequence group. Further, premotor mu asymmetry before task exposure predicted sequence acquisition, such that participants with longer baseline trough phases acquired greater skill and showed larger learning-related increases in mu peak-trough symmetry. Overall, these findings provide first evidence that motor sequence learning reshapes premotor mu rhythms, consistent with learning-related redistribution of cortical excitability across the mu cycle.

Significance statement

Motor sequence learning requires coordinated activity between premotor and sensorimotor cortices. Although sensorimotor mu rhythm phase gates LTP-like corticospinal plasticity, the effects of TMS on motor learning, and learning-related plasticity, the role of premotor mu waveform shape in motor sequence learning is unknown. Using cycle-by-cycle analysis, we characterized mu peak-trough symmetry recorded over premotor regions before, during, and after healthy adults learned an implicit motor sequence or completed a control task. We found that premotor mu peak-trough symmetry progressively increased during learning, with baseline asymmetries and learning-related symmetry increases both predicting sequence learning. Our findings suggest that sequence learning redistributes excitability across the mu cycle and identify premotor mu rhythm waveform shape as a novel marker of motor sequence learning.

Introduction

Motor sequence learning recruits distributed cortical networks that encode, plan, and precisely execute complex movement sequences (Diedrichsen & Kornysheva, 2015; Krakauer et al., 2019). Within these networks, premotor cortex (PMC) activity encodes sequence-specific knowledge that progressively stabilizes during learning (Ariani & Diedrichsen, 2019; Berlot et al., 2020; Yokoi & Diedrichsen, 2019). In addition, PMC activity directly supports voluntary hand control and movement execution through its dense corticocortical projections with the primary motor cortex (M1) (Davare et al., 2008; Dum & Strick, 2005; He et al., 1993; Turrini et al., 2023). PMC activity thus encodes and maintains sequence-specific representations during motor sequence learning while also supporting the execution of learned sequences.

Neuronal populations in sensorimotor cortical areas, including the primary and premotor cortex exhibit mu (8-13 Hz) oscillatory activity (Gallese et al., 1996; Haegens et al., 2011; Hussain et al., 2019; Kuhlman, 1978; Pfurtscheller et al., 2006; Rizzolatti et al., 1996; Suresh & Hussain, 2023). Single neuron firing rates (Haegens et al., 2011), corticospinal output (Bergmann et al., 2019; Hussain et al., 2019; Suresh & Hussain, 2023; Wischniewski et al., 2022), corticospinal plasticity (Baur et al., 2020; Zrenner et al., 2018), and interhemispheric communication (Stefanou et al., 2018) are all increased during mu rhythm trough relative to peak phases. Furthermore, delivering TMS interventions to the primary motor cortex (M1) during mu trough phases enhances offline motor sequence learning (Hussain et al., 2021), suggesting that these phases reflect brief windows of heightened sensorimotor cortical excitability during which exogenous stimulation maximally promotes consolidation. In contrast, corticospinal plasticity elicited by sequence-specific learning is most prominent during mu peak phases (Suresh et al., 2025), which may protect newly-formed sequence memories from interference during early consolidation. These prior studies (Baur et al., 2020; Hussain et al., 2019, 2021; Suresh et al.,

2025; Zrenner et al., 2018) all treated mu rhythm peaks and troughs as distinct phases with unique neurophysiological properties. However, mu peak and trough phases are continuous in time (Cole & Voytek, 2017; Jones et al., 2009; Schaworonkow, 2025), and treating them as independent may overlook interactions between phases that are better captured with more holistic waveform shape metrics.

The mu rhythm is characterized by its asymmetric shape, with sharper peaks than troughs (Cole & Voytek, 2017; Kuhlman, 1978; Pfurtscheller & Aranibar, 1979; Schaworonkow, 2025). These relatively sharper mu peaks have been proposed to reflect rapid, synchronous layer V pyramidal neuronal voltage changes caused by shifts in the excitatory-inhibitory balance of thalamocortical inputs (Buzsáki et al., 2012; Hughes & Crunelli, 2005; Pineda, 2005). However, waveform shape is typically overlooked by conventional Fourier-based analytical methods, which assume that neural oscillations are comprised solely of sinusoidal subcomponents. This assumption neglects the reality that brain oscillations exhibit complex, non-sinusoidal waveforms generated by non-uniform phase distributions (Cole & Voytek, 2017; Cole & Voytek, 2019; Jones, 2016; Schaworonkow et al., 2018). Waveform shape metrics like peak-trough symmetry directly measure these characteristics. Indeed, prior studies within (Opie et al., 2025; Szul et al., 2023) and outside the motor domain have shown that waveform shape covaries with changes in cortical excitation-inhibition balance and memory performance in animal models (Trimper et al., 2014) as well as neurostimulation-induced changes in visual perception in humans (Marshall et al., 2022). Despite the mu rhythm's established role in voluntary motor behavior and its known deviation from a pure sinusoid, the functional role of mu waveform shape in motor learning remains unknown.

Here, we addressed this gap in knowledge by evaluating the effects of motor sequence learning on mu rhythm waveform shape (i.e., peak-trough symmetry) using oscillatory activity recorded over human premotor regions. Given PMC's established role in motor sequence learning (Ariani et al., 2025; Diedrichsen & Kornysheva, 2015; Kornysheva & Diedrichsen, 2014; Yokoi & Diedrichsen, 2019) and our prior findings implicating both sensorimotor cortical mu peak and trough phases in sequence learning (Hussain et al., 2021; Suresh et al., 2025), we hypothesized that motor sequence learning would alter premotor mu peak-trough symmetry. Because cortical excitability is enhanced during mu trough phases (Haegens et al., 2011), changes in peak-trough symmetry could feasibly reflect learning-related redistribution of excitability across the mu cycle. To test our hypothesis, we used cycle-by-cycle waveform shape analysis to characterize mu peak-trough symmetry before, during, and after healthy adults learned a motor sequence or completed a similar task that produced no sequence learning. We found that premotor mu peak-trough symmetry progressively increased during motor sequence learning. Further, both baseline mu asymmetries and learning-related changes in symmetry positively predicted sequence acquisition skill. Overall, our results are consistent with the notion that motor sequence learning redistributes excitability across the mu cycle and identify premotor mu rhythm waveform shape as a novel marker of human motor sequence learning.

Methods

Participants

Thirty-six naïve right-handed healthy adult participants (sequence group: N = 18, 20 ± 0.37 years, 13 F and 5 M; no-sequence group: N=18, 21.8 ± 0.94 years, 12 F and 6 M) participated in a single-session study. Right-handedness was verified using the Edinburgh Handedness

Inventory (Oldfield, 1971). The Institutional Review Board at the University of Texas at Austin approved all procedures and participants provided their written informed consent before participation. Participants were randomly assigned to either the sequence group or the no-sequence group prior to starting the experiment. This sample size was chosen based on previous studies demonstrating significant mu phase-dependent variation in learning-related corticospinal plasticity and phase-dependent enhancement of motor sequence learning (N = 16-18; Hussain et al., 2021; Suresh et al., 2025).

[Figure 1 goes here]

Experimental design and timeline

After EEG preparation, baseline resting EEG was recorded while participants sat quietly with their eyes open. Participants then practiced one of two versions of the serial reaction time task during acquisition (SRTT; see below for details). Although EEG was recorded during task performance, task-related EEG signals were not analyzed and are thus not reported here. Resting EEG was also recorded immediately and 30 minutes after acquisition; all resting EEG recordings were 3 minutes in duration. Following each recording, participants received mu phase-dependent and phase-independent single-pulse TMS to evaluate changes in corticospinal output; these data were reported previously (Suresh et al., 2025) and are not further analyzed here. One hour after acquisition, both groups completed a brief retention test using the same version of the task experienced during acquisition. After retention testing, all participants completed the Process Dissociation Procedure (PDP; Wilkinson & Shanks, 2004) to assess explicit sequence awareness. See Figure 1A for experimental design and timeline.

Data Acquisition

EEG acquisition. EEG was recorded using 64-channel TMS-compatible amplifiers (NeuroOne Tesla with real-time digital out option, Bittium Biosignals, Finland). Impedances were maintained

below 10 k Ω . EEG signals were sampled at 5 kHz, with low-pass hardware filtering at 1250 Hz and a resolution of 0.001 μ V.

Serial Reaction Time Task (SRTT). Participants performed either a sequence or a no-sequence version of the SRTT (Nissen & Bullemer, 1987; Perez et al., 2007) implemented in E-Prime 3 (Psychology Software Tools). Participants were seated in front of a computer monitor with their right arm resting comfortably on a tabletop and their right hand placed on a serial response box (Chronos Response Device, Psychology Software Tools, see Figure 1B). In this study, the no-sequence group provides a control condition that experimentally accounts for non-specific effects of motor sequence execution (including repeated keypresses) on waveform shape. During the SRTT, the monitor displayed four equally spaced green dashes on a black background. On each trial, one of the dashes was replaced by a circular target. Before starting the task, participants were instructed to respond to the circular target's appearance as quickly and accurately as possible by pressing the spatially corresponding button with the appropriate finger of their right hand, as illustrated in Figure 1B. Correct responses made the circular target disappear, completing the trial. Incorrect responses left the circular target visible on the monitor until the participant pressed the correct button. An inter-trial interval of 500 ms separated successive trials. Participants did not receive any additional feedback regarding accuracy or speed.

Following a familiarization block that included 10 trials (data not shown), participants in the sequence group performed 14 blocks of keypresses with one-minute rest intervals. Each block consisted of 10 repetitions of a 12-element sequence (totaling 120 keypresses/block). Blocks 3-7 and 9-13 incorporated a fixed 12-element sequence (2-3-1-4-3-2-4-1-3-4-2-1), whereas blocks 1, 2, 8, and 14 were random blocks that contained no sequence. During retention testing,

participants in the sequence group completed 7 blocks of 120 keypresses with one-minute rest intervals between blocks. Blocks 1 and 7 were random, while blocks 2-6 contained the same fixed 12-element sequence presented during acquisition. Random blocks did not contain consecutive item repeats, and each element appeared at the same approximate frequency. In contrast, participants in the no-sequence group performed randomized keypresses during all blocks. Participants in each group did not receive any information about the presence, absence, length, or structure of the embedded sequence.

Process Dissociation Procedure (PDP). Following retention, participants completed the PDP. The PDP evaluates explicit control over sequence knowledge that may emerge during implicit SRTT practice (Destrebecqz et al., 2005; Wilkinson et al., 2009, 2015; Wilkinson & Jahanshahi, 2007; Wilkinson & Shanks, 2004) and operates on the principle that explicit knowledge is both verbalizable on demand and subject to voluntary control. The PDP consists of an inclusion and exclusion component. Each component presents 12 unique three-element fragments derived from the 12-element sequence embedded in the sequence version of the SRTT (e.g., 2-3-1, 3-1-4, 1-4-3, etc.). The inclusion component measures verbalizable and consciously accessible knowledge. During inclusion trials, participants were presented with two elements of each three-element fragment and were asked to generate the subsequent element by pressing the correct key. The exclusion component measures voluntary control. During exclusion trials, participants viewed the first two elements of the three-element fragment but were instructed to refrain from generating the next element by pressing any key except the one corresponding to the next element in the fragment. Before completing the inclusion and exclusion components of the PDP, participants were informed that element repetitions (i.e., a 2 immediately after a 2) were prohibited. Each inclusion trial had a 1/3 probability of guessing a correct response by chance, whereas each exclusion trial had a 2/3 probability of guessing a correct response by chance.

The order of inclusion and exclusion components was counterbalanced across participants per group.

Data Analysis

SRTT. For the SRTT, reaction times (RTs) were averaged within each block. We defined acquisition skill as the difference between the mean RT of the last random block and the mean RT of the last sequence block during acquisition testing. We defined retention skill as the difference between the mean RT of the first random block and the mean RT of the first sequence block during retention testing.

$$\text{Acquisition skill} = \text{RT } \textit{Acquisition}_{\text{block 14}} - \text{RT } \textit{Acquisition}_{\text{block 13}}$$

$$\text{Retention skill} = \text{RT } \textit{Retention}_{\text{block 1}} - \text{RT } \textit{Retention}_{\text{block 2}}$$

PDP. Inclusion trial responses were considered accurate when participants correctly completed the three-element fragment by selecting the correct key in the sequence. Exclusion trial responses were considered accurate when participants successfully avoided the fragment's next element by selecting one of the two alternative keys. We compared the total number of accurate trials in the inclusion and exclusion conditions against their respective chance levels (i.e., 4/12 for the inclusion test and 8/12 for the exclusion test) to assess explicit awareness of the embedded sequence.

EEG preprocessing. Resting EEG signals were processed using MNE Python (Gramfort et al., 2013) and custom-written Python scripts. To minimize anticipatory effects associated with re-starting the SRTT task at the end of each EEG recording, we excluded the last 5 seconds of

each resting EEG recording from analysis. Inter-block resting EEG segments (i.e., between SRTT blocks) were automatically identified by detecting gaps longer than 55 seconds between consecutive keypresses. To minimize the influence of post-practice fatigue and anticipatory effects of re-starting practice during the next practice block, the first and last 5 seconds of each inter-block resting EEG recording were also excluded from analysis.

Bad channels were visually identified and interpolated using spherical splines. EEG signals were then band-pass filtered between 1-50 Hz using a zero-phase, non-causal finite impulse response (FIR) filter with a Hamming window. Filtered data were then re-referenced to the common average reference (CAR), and re-referenced EEG signals were segmented into 1-second non-overlapping epochs. Independent Component Analysis (ICA) was used to identify non-neural EEG artifacts using the *fastica* algorithm (maximum iterations = 800). ICA components reflecting eye blinks, eye movements, and electrode noise artifacts were visually identified and rejected; remaining components were back-projected to EEG sensor space. On average, 5.06 ± 0.29 bad channels were identified and interpolated and 8.61 ± 0.43 independent components were rejected. After ICA, all EEG epochs were visually reviewed, and those containing excessive noise or residual artifacts not attenuated by ICA were manually rejected. On average, 4.56 ± 0.66 epochs during baseline, pre- and post-SRTT resting EEG recordings and 18.26 ± 2.69 epochs during inter-block rest intervals were rejected. After preprocessing, all remaining EEG epochs were forwarded to waveform shape analysis. Inter-block resting EEG from two subjects (one per group) could not be obtained due to recording failure and were therefore excluded from analyses.

EEG waveform shape analysis. A subset of channels overlying left premotor cortex (FC3, F1, F5, C1, C5) and right-parieto-occipital cortex (PO4, Pz, P4, Iz, PO8) were selected for further analysis. FC3 and four surrounding electrodes were chosen as the primary region of interest

given FC3's approximate location overlying the left PMC (Scrivener & Reader, 2022; Zrenner et al., 2022). PO4 and four surrounding electrodes were chosen as the control site, given PO4's approximate location overlying visual cortical regions which do not directly contribute to motor sequence planning or encoding (Scrivener & Reader, 2022; Whitlock, 2017). For each region of interest, data recorded from the central channel was Hjorth-transformed by subtracting the average of each channel's four surrounding channels (left premotor center = FC3 [center], F1, F5, C1, C5 [surround]; right parieto-occipital center = PO4 [center], Pz, P4, Iz, PO8 [surround]). This spatial filtering approach attenuates the effects of volume conduction and enhances the signal-to-noise ratio of local EEG features (Hjorth, 1975). Resulting Hjorth-transformed signals were then demeaned and linearly detrended. Next, Hjorth-transformed data were spectrally decomposed using Welch's method (1-50 Hz with 1 Hz resolution using a Hann window with non-overlapping 1 second segments), and the resulting power spectra were averaged across all baseline epochs (Figure 2A, 2C and Supplemental Figure S1). The resulting mean power spectrum was then parametrized using *specparam* (Donoghue et al., 2020) to confirm the presence of periodic mu-alpha oscillations at FC3 and PO4 and to isolate periodic mu-alpha power from aperiodic activity (*specparam* parameters: maximum number of peaks = 4, minimum peak height = 0.1, aperiodic mode = 'fixed'). That is, we subtracted each participant's modeled aperiodic (1/f) component from their corresponding *specparam*-modeled power spectrum at baseline (Figure 2B, 2D and Supplemental Figure S2). Peak periodic mu-alpha power was calculated from FC3 and control regions as the maximum power value within the periodic spectrum in the 8-13 Hz range. One participant in the sequence group exhibited minimal FC3 periodic mu-alpha power at baseline ($<0.001 \mu V^2/Hz$), precluding reliable mu peak-trough symmetry measurements; this participant was excluded from all subsequent analyses.

[Figure 2 goes here]

To characterize mu-alpha waveform shape for each region (i.e., FC3 and control), we used the *ByCycle* algorithm (Cole & Voytek, 2019). This algorithm divides timeseries oscillatory activity into individual cycles by identifying peaks, troughs and zero-crossings within a pre-defined frequency band of interest (here, mu-alpha [8-13 Hz], see Figure 3A). Each cycle's mid-points are identified as those timepoints at which the cycle's voltage is half of the adjacent cycle's peak and trough voltages. After identifying individual cycles, *ByCycle* measures features of each cycle. Because neural oscillations are rarely present throughout an entire EEG recording, *ByCycle* also determines if a given cycle is part of a larger oscillatory episode (see Figure 3B). To ensure that our analysis focused only on oscillatory episodes, we used established mu-alpha rhythm oscillatory episode detection parameters (see Supplemental Table S1; Bender et al., 2025; Cole & Voytek, 2019; Donoghue et al., 2020; García-Rosales et al., 2024). All subsequent analyses were restricted to oscillatory episodes detected using these parameters.

[Figure 3 goes here]

For each time point, we extracted mu-alpha oscillatory amplitude, period, and peak-trough symmetry for each region. These parameters were then averaged across all oscillatory episodes per time point and forwarded to statistical analyses. Peak-trough symmetry was calculated as the fraction of the oscillatory period corresponding to the peak phase (ranging between 0 and 1, with 0.5 reflecting perfect symmetry). To calculate deviation from a perfect sinusoid and to facilitate interpretability, we subtracted 0.5 from all raw peak-trough symmetry values (Bender et al., 2025; García-Rosales et al., 2024; Schaworonkow & Voytek, 2021). Resulting normalized peak-trough symmetry values range from -0.5 to 0.5, with negative values reflecting a trough bias and positive values reflecting a peak bias (see Figure 3C). We also calculated Δ peak-trough symmetry as the difference between peak-trough symmetry values obtained at each post-acquisition timepoint (Post0 or Post30) and the corresponding baseline

value for each participant and region. This metric quantified the extent to which mu-alpha peak-trough symmetry changed following SRTT acquisition.

Statistical analysis

Statistical analyses were performed in R (version 4.5.0, R Core Team, 2025; Wickham, 2016; Wickham et al., 2026; Kuznetsova et al., 2017). Given that waveform shape measures are influenced by underlying changes in oscillatory frequency and power and that cycle-by-cycle features are temporally autocorrelated (Cole & Voytek, 2018), all statistical models evaluating mu-alpha waveform shape included mu-alpha oscillatory AMPLITUDE and PERIOD as covariates. Model fits and assumptions, including normality of residuals and homoscedasticity, were assessed using histograms of residuals and quantile-quantile plots. When model residuals deviated significantly from normality, we used non-parametric bootstrapping (1000 iterations) to obtain robust model coefficients and 95% confidence intervals (Davison & Hinkley, 1997). F-tests with Satterthwaite's approximation were used to evaluate each factor's significance. In the event of a significant three-way interaction, post hoc two-way models were performed. In the event of a significant two-way interaction, post hoc pairwise comparisons were performed. Alpha was 0.05 for all comparisons, and p-values were corrected for multiple comparisons using Tukey's Honestly Significant Difference test where appropriate. A full description of each statistical model is provided in Supplemental Table S2.

First, we evaluated changes in mean RT during acquisition and retention using linear mixed effects models. Statistical models included BLOCK (acquisition blocks 1-14, retention blocks 1-7), GROUP (sequence, no-sequence), their two-way interactions as fixed effects. Mean RT was the response variable and individual participants was included as random intercepts. To evaluate differences in acquisition and retention skill between groups, we used unpaired t-tests.

To assess explicit sequence awareness, we compared fragment completion accuracy to chance using separate single-sample right-tailed t-tests for the inclusion and exclusion components. One participant in the no-sequence group did not complete the PDP.

Next, we evaluated changes in mu-alpha peak-trough symmetry from baseline to immediately and 30 minutes after acquisition across groups, again using a linear mixed effects model. The model included GROUP (sequence, no-sequence), TIME (baseline, Post0, and Post30), REGION (FC3, control), their two- and three-way interactions as fixed effects, individual participants as random intercepts, and mu-alpha peak-trough symmetry as the response variable. We also evaluated changes in mu-alpha peak-trough symmetry during acquisition inter-block rest intervals; this model included GROUP (sequence, no-sequence), BLOCK (1-13), REGION (FC3, control), their two- and three-way interactions as fixed effects, individual participants as random intercepts, and mu-alpha peak-trough symmetry again as the response variable. To further characterize the spatial specificity of changes in mu-alpha peak-trough symmetry during inter-block rest periods, we performed an exploratory whole-scalp analysis using the same model structure. Specifically, we Hjorth-transformed mu-alpha signals recorded from all scalp electrodes and then fit a separate linear mixed effects model for each electrode. Due to the exploratory nature of this analysis, no correction for multiple comparisons was performed. To characterize the extent to which mu-alpha activity deviated from perfect symmetry, we compared mu-alpha peak-trough symmetry to zero using separate single-sample t-tests for each region.

We also evaluated relationships between changes in mu-alpha peak-trough symmetry and sequence-specific learning measured during acquisition and retention using linear regression

models. Δ PEAK-TROUGH SYMMETRY was defined as the difference between peak-trough symmetry at each post-acquisition timepoint (Post0 or Post30) and the corresponding baseline peak-trough symmetry value for each participant and region. Each model included GROUP (sequence, no-sequence), Δ PEAK-TROUGH SYMMETRY (continuous variable), time (baseline, Post0, and Post30) and their two- and three-way interactions as fixed effects. Acquisition skill and retention skill were the response variables for each model, respectively. To reduce model complexity and facilitate interpretability, separate models were fit for each region of interest (FC3, control).

We then tested whether baseline FC3 μ peak-trough symmetry predicted sequence-specific learning using separate linear regression models for acquisition and retention. Here, each model included sequence-specific skill (acquisition or retention skill) as the response variable and BASELINE PEAK-TROUGH SYMMETRY (continuous variable), GROUP (sequence, no-sequence) and their two-way interaction as fixed effects. Pearson's correlations were used to quantify the relationship between μ -alpha peak-trough symmetry and skill.

Finally, to confirm that learning-related changes in FC3 μ peak-trough symmetry were not due to changes in oscillatory amplitude or period, we used separate linear mixed effects models to evaluate changes in these parameters over time. Each model included GROUP (sequence, no-sequence), TIME (baseline, Post0, Post30), and their two-way interaction as fixed effects, with μ -alpha oscillatory amplitude and period as response variables, respectively. Individual participants were included as random intercepts for all models. Similar models were used for inter-block rest interval analyses, with BLOCK (1-13) as a fixed effect instead of TIME. To verify that the percentage of cycles identified as oscillatory episodes did not differ between groups or

across timepoints, we also compared FC3 mu oscillatory burst percentage across groups and time points using the same modeling approach.

Results

Participants in the sequence group showed sequence-specific improvements in reaction time

During SRTT acquisition, participants in both the sequence and no-sequence groups decreased their mean RTs across blocks (Figure 4A, main effect of BLOCK: $F_{(13, 429)} = 12.56$, $p < 0.001$). However, participants in the sequence group showed faster mean RTs during the sequence blocks than the no-sequence group during the same blocks (BLOCK x GROUP interaction: $F_{(13, 429)} = 9.06$, $p < 0.001$; no main effect of GROUP: $F_{(1, 33)} = 0.56$, $p = 0.45$). Post hoc pairwise comparisons revealed that mean RTs did not differ between groups during the early sequence blocks (blocks 3-7, $t < 1.46$, $p > 0.15$) but were significantly faster in the sequence than the no-sequence group during late sequence blocks (blocks 11-13, $t > 2.01$, $p < 0.04$). For the sequence group, mean RTs were faster during the last sequence block than the last random block (block 13 vs. 14, $\beta = -96.73$, $t_{(429)} = -8.07$, $p < 0.001$), but this was not the case for the no-sequence group ($\beta = 1.95$, $t_{(429)} = 0.16$, $p > 0.99$). Finally, acquisition skill was significantly greater in the sequence than the no-sequence group (Figure 4B, $t_{(33)} = 5.02$, $p < 0.001$, mean difference = 98.69 ± 19.64 ms), indicating that participants in the sequence group experienced sequence-specific learning.

During retention, participants in both groups decreased their mean RTs across blocks (Figure 4A, main effect of BLOCK: $F_{(6, 198)} = 18.19$, $p < 0.001$), and mean RTs were overall faster for the sequence group than the no-sequence group (main effect of GROUP: $F_{(1, 33)} = 5.96$, $p = 0.02$). Mean RTs did not differ between groups during random blocks but were significantly faster for

the sequence than the no-sequence group during sequence blocks (GROUP $\times$ BLOCK interaction: $F_{(6, 198)} = 20.36$, $p < 0.001$). Post-hoc pairwise comparisons revealed that mean RTs were faster in the sequence group than in the no-sequence group during sequence blocks 2-6 ($t_{(52.3)} > 2.8$, $p < 0.007$) but similar during random blocks 1 and 7 ($t_{(52.3)} < 1.16$, $p > 0.24$). In addition, retention skill was significantly greater in the sequence than the no-sequence group (Figure 4B, $t_{(33)} = 5.29$, $p < 0.001$, mean difference = 87.83 ± 16.59 ms), indicating that participants in the sequence group retained sequence-specific skill over time.

[Figure 4 goes here]

No evidence of explicit sequence knowledge in either group

In the sequence group, mean fragment completion accuracies during PDP task performance were greater than chance for the inclusion component (Supplemental Figure S3, 6 ± 0.7 , $t_{(16)} = 2.84$, $p = 0.01$, chance = 4) but not the exclusion component (7.82 ± 0.56 , $t_{(16)} = -0.31$, $p = 0.75$, chance = 8). In the no-sequence group, fragment completion accuracies were not greater than chance for either component (inclusion = 3.88 ± 0.45 , exclusion = 7.7 ± 0.54 , $t < 0.53$ for both, $p > 0.59$ for both). Given that explicit awareness requires both conscious knowledge of the sequence and the ability to intentionally control sequence production, we found no strong evidence of explicit sequence awareness in either group.

FC3 mu rhythms progressively shift towards peak phases during motor sequence learning

We characterized FC3 mu-alpha peak-trough symmetry using resting EEG recordings obtained at baseline, immediately (Post0), and thirty minutes after (Post30) SRTT acquisition. FC3 mu-alpha peak-trough symmetry did not change after acquisition in either group (no effect of

GROUP: $F_{(1,34.06)} = 2.10$, $p = 0.15$, TIME: $F_{(2,163.62)} = 0.48$, $p = 0.61$, GROUP x TIME interaction: $F_{(2, 162.35)} = 0.48$, $p = 0.61$, or GROUP x TIME x REGION interaction: $F_{(2,162.46)} = 0.03$, $p = 0.96$). However, FC3 mu rhythms were significantly more biased towards trough phases than alpha rhythms recorded over the control site (Figure 5, main effect of REGION: $F_{(1,187.08)} = 39.28$, $p < 0.001$, $\beta_{observed} = 0.02$, $t = 3.80$, $p = 0.0001$, 95% $CI_{bootstrapped} = [0.013, 0.039]$). Single-sample t -tests confirmed that FC3 mu rhythms deviated significantly from a perfect sinusoid, towards trough phases (mean = -0.0087, 95% $CI = [-0.013, -0.004]$, $t_{(34)} = -3.85$, $p = 0.0004$). In contrast, PO4 alpha rhythms also deviated from a perfect sinusoid, towards peak phases (mean = 0.012, 95% $CI = [0.007, 0.018]$, $t_{(34)} = 4.71$, $p < 0.001$). This result is consistent with prior reports that mu rhythms are typically asymmetric (Cole & Voytek, 2017; Kuhlman, 1978).

[Figure 5 goes here]

We then evaluated changes in mu-alpha peak-trough symmetry across inter-block rest intervals during acquisition. This analysis revealed that changes in mu-alpha peak-trough symmetry differed across both groups and regions (Figure 6; significant GROUP x BLOCK x REGION interaction, $F_{(1, 812.91)} = 5.27$, $p = 0.02$). Post-hoc contrasts confirmed that FC3 mu peak-trough symmetry increased more in the sequence group than in the no-sequence group ($\beta = 0.0014$, $t_{(814)} = 2.02$, $p = 0.04$), and that this group difference was significantly stronger at FC3 than at the control site ($\beta = 0.002$, $t_{(813)} = 2.29$, $p = 0.02$). To further characterize this three-way interaction, we fit a separate post hoc linear mixed effects model for each region. For FC3, participants in the sequence group showed larger increases in peak-trough symmetry than those in the no-sequence group (significant GROUP x BLOCK interaction, $F_{(1, 391.95)} = 4.40$, $p = 0.03$; sequence group: $\beta = 0.0010$, 95% $CI = [0.000089, 0.00200]$, no-sequence group: $\beta = -0.00038$, 95% $CI = [-0.00131, 0.00055]$). For the control site, peak-trough symmetry changed similarly over time in both groups (main effect of BLOCK, $F_{(1, 396.97)} = 4.35$, $p = 0.03$; no main effect of GROUP, $F_{(1, 183.91)} = 0.29$, $p = 0.59$; no GROUP x BLOCK interaction, $F_{(1, 391.32)} = 1.5$, p

= 0.22). Overall, increases in FC3 mu peak-trough symmetry across inter-block rest intervals were greater in the sequence group than in the no-sequence group.

FC3 mu oscillatory amplitude and period do not change systematically during learning

To verify that learning-related increases in FC3 mu peak-trough symmetry were not driven by changes in oscillatory amplitude or period, we also examined how these parameters changed over time. For pre- and post-acquisition resting EEG recordings, there were no differences in either amplitude or period across time for either group ($F < 1.9$, $p > 0.15$ for all comparisons). For inter-block rest intervals, period also did not change across blocks in either group ($F < 0.7$, $p > 0.4$ for all comparisons). Both groups showed progressive increases in amplitude across inter-block rest intervals (main effect of BLOCK: $F_{(1, 392)} = 4.0$, $p = 0.045$), but no GROUP $\times$ BLOCK interaction ($F_{(1, 392)} = 2.78$, $p = 0.095$). Participants in the no-sequence group showed greater overall FC3 mu amplitude than those in the sequence group (main effect of GROUP: $F_{(1, 37.46)} = 4.43$, $p = 0.04$), reflecting a pre-existing group difference in baseline mu amplitude that was stable across blocks. In addition, mu oscillatory burst percentage did not differ between groups nor did it change over time (no main effect of GROUP, TIME or GROUP $\times$ TIME interaction, $F < 0.8$, $p > 0.45$ for all comparisons). Finally, mu-alpha power extracted at each participant's peak frequency did not differ between groups or across time (Supplemental Figure S4; $F < 1.07$, $p > 0.3$ for all comparisons). Similarly, mu-alpha amplitude at the individual peak frequency during inter-block rest intervals also did not differ between groups (no GROUP $\times$ BLOCK or GROUP $\times$ BLOCK $\times$ REGION effect, $F < 1.14$, $p > 0.28$). Together, these results indicate that learning-related changes in mu peak-trough symmetry were not driven by systematic changes in mu oscillatory amplitude, period, or the percentage of detected mu oscillatory episodes.

[Figure 6 goes here]

Changes in FC3 mu waveform shape reflect sequence-specific skill acquisition

Although FC3 mu peak-trough symmetry did not differentially change between groups after SRTT acquisition (see Figure 5), we identified a greater increase in FC3 mu peak-trough symmetry during inter-block rest intervals for the sequence group relative to the no-sequence group (Figure 6). We therefore fit separate linear regression models to determine whether learning-related changes in peak-trough symmetry predicted acquisition skill in each region. As shown in Figure 4, the sequence group showed greater acquisition skill than the no-sequence group (main effect of GROUP: $F_{(1,59)} = 78.84$, $p < 0.001$, $\beta = 93.06$, $t = 5.71$, $p < 0.001$). The relationship between changes in FC3 mu peak-trough symmetry and acquisition skill was also significantly stronger for the sequence than the no-sequence group. This difference was present both immediately and 30 minutes after acquisition (see Figure 7A, no main effect of TIME: $F_{(1,59)} = 0.07$, $p = 0.77$, GROUP x Δ PEAK-TROUGH SYMMETRY interaction: $F_{(1,59)} = 21.81$, $p < 0.001$, $\beta_{\text{observed}} = -1915.46$ ms, $t = -3.28$, $p = 0.001$, 95% $CI_{\text{bootstrapped}} = [-3857.90, -1170.32]$; no GROUP x Δ PEAK-TROUGH SYMMETRY x TIME interaction: $F_{(1,59)} = 0.18$, $p = 0.66$). However, the relationship between changes in control site peak-trough symmetry and acquisition skill did not differ between groups (Figure 7B, no main effect of Δ PEAK-TROUGH SYMMETRY: $F_{(1,59)} = 0.09$, $p = 0.75$, TIME: $F_{(1,59)} = 0.001$, $p = 0.97$, GROUP x Δ PEAK-TROUGH SYMMETRY interaction: $F_{(1,59)} = 0.02$, $p = 0.88$ or GROUP x Δ PEAK-TROUGH SYMMETRY x TIME interaction: $F_{(1,59)} = 0.27$, $p = 0.60$).

To test whether changes in mu peak-trough symmetry also related to retention skill, we again used linear regression. As expected, the sequence group showed greater retention skill than the no-sequence group (Supplemental Figure S5, main effect of GROUP: $F_{(1,59)} = 51.49$, $p < 0.001$, β

= 85.47 ms, $t = 4.72$, $p < 0.001$). However, the relationship between mu-alpha peak-trough symmetry and retention skill did not differ between groups for either FC3 or the control site ($F < 0.32$ and $p > 0.57$ for all main and interaction effects).

We also examined the spatial specificity of learning-related changes in mu-alpha peak-trough symmetry. Specifically, we applied exploratory linear mixed effects models to Hjorth-transformed mu-alpha peak-trough symmetry obtained from all scalp electrodes. Only FC3, FC5, and O2 showed significant changes in mu-alpha peak-trough symmetry across inter-block rest intervals (Supplemental Figure S6, significant GROUP $\times$ BLOCK interaction: FC3: $\beta = 0.0014$, $t = 2.29$, $p = 0.0224$; FC5: $\beta = -0.0014$, $t = -2.18$, $p = 0.02$; O2: $\beta = 0.0013$, $t = 2.10$, $p = 0.03$). Exploratory Pearson's correlation analyses showed that changes in mu-alpha peak-trough symmetry were only positively associated with acquisition skill at FC3 (FC3: $r_{(17)} = 0.77$, $R^2 = 0.6$, $p = 0.0002$; FC5: $r_{(17)} = -0.45$, $R^2 = 0.21$, $p = 0.06$; O2: $r_{(17)} = -0.1$, $R^2 = 0.01$, $p = 0.69$), indicating that mu-alpha waveform shape changes predicted sequence learning at FC3 only.

[Figure 7 goes here]

Baseline FC3 mu peak-trough symmetry predicts sequence-specific learning

Our analyses revealed that learning-related changes in FC3 mu peak-trough symmetry were associated with acquisition skill. We next examined whether a relationship between FC3 waveform shape and acquisition existed *before* any task exposure. Linear regression showed that the relationship between baseline FC3 mu peak-trough symmetry and acquisition skill differed significantly between groups (Figure 8, main effect of PEAK-TROUGH SYMMETRY: $F_{(1,29)} = 11.48$, $p = 0.002$; main effect of GROUP: $F_{(1,29)} = 30.66$, $p < 0.001$; significant PEAK-TROUGH SYMMETRY $\times$ GROUP interaction: $F_{(1,29)} = 5.37$, $p = 0.02$, $\beta = 1186.13$, 95%

$CI_{bootstrapped} = [667.28, 4587.63]$). This difference was driven by a significantly stronger negative relationship between baseline FC3 peak-trough symmetry and acquisition skill for the sequence group than the no-sequence group (Figure 8). We also evaluated whether baseline FC3 mu peak-trough asymmetry predicted retention skill. As expected, linear regression showed that the sequence group gained greater retention skill than the no-sequence group (main effect of GROUP: $F_{(1,29)} = 25.44, p < 0.001, \beta = -81.24, t = -3.95, p = 0.0004$). However, FC3 peak-trough asymmetry did not predict retention skill for either group (no main effect of peak-trough symmetry: $F_{(1,29)} = 0.47, p = 0.49$, no GROUP x PEAK-TROUGH SYMMETRY interaction: $F_{(1,29)} = 0.03, p = 0.86$). Similarly, baseline mu-alpha peak-trough symmetry at the control site did not predict acquisition skill in either group (no main effect of PEAK-TROUGH SYMMETRY: $F_{(1,29)} = 0.10, p = 0.75$; or PEAK-TROUGH SYMMETRY x GROUP interaction: $F_{(1,29)} = 0.48, p = 0.49$). Again, as expected, the sequence group showed greater acquisition skill than the no-sequence group (main effect of GROUP: $F_{(1,29)} = 23.26, p < 0.001$). Overall, baseline FC3 mu peak-trough symmetry predicted acquisition but not retention skill.

[Figure 8 goes here]

Next, to determine if sequence group participants with a greater baseline mu trough bias showed larger learning-related shifts towards mu peak phases (i.e., greater increases in peak-trough symmetry), we regressed baseline FC3 mu peak-trough asymmetry against learning-related changes in mu peak-trough symmetry using a linear model. This analysis revealed a strong negative relationship (Figure 9, $r_{(17)} = -0.81, p < 0.001, R^2 = 0.66$), such that participants with a greater baseline FC3 mu trough bias exhibited larger shifts toward FC3 mu peak phases after SRTT acquisition.

Finally, to verify that the relationships between baseline mu peak-trough symmetry, acquisition skill, and learning-related changes in peak-trough symmetry were not driven by influential observations, we conducted a sensitivity analysis using Cook's distance (threshold: 4/N). Removing influential observations did not change the direction or significance of either result (see Supplemental Table S3). Overall, these robust relationships suggest that baseline and learning-related changes in mu peak-trough symmetry reflect the same underlying neurophysiological mechanism.

[Figure 9 goes here]

Discussion

We (Hussain et al., 2019; Suresh & Hussain, 2023) and others (Baur et al., 2020; Bergmann et al., 2019; Wischniewski et al., 2022; Zrenner et al., 2018) previously showed that sensorimotor mu phase gates corticospinal transmission, LTP-like plasticity, the effects of TMS on motor learning, and learning-related plasticity. Specifically, M1 TMS interventions delivered during sensorimotor mu trough phases enhance motor sequence learning (Hussain et al., 2021), while motor sequence learning elicits mu peak-specific corticospinal plasticity (Suresh et al., 2025). These findings implicate both mu peaks and troughs in motor sequence learning. To better understand these mechanisms, here we evaluated learning-related changes in the waveform shape of mu rhythms recorded over left premotor regions. We used cycle-by-cycle analysis of resting EEG data acquired before, during, and after motor sequence learning. Our results show that (1) mu rhythms recorded over premotor regions become more symmetric during motor sequence learning by shifting towards peak phases, (2) learning-related increases in mu symmetry are associated with better sequence learning, and (3) baseline mu asymmetry predicts sequence learning and learning-related symmetry increases. These findings provide

first evidence that motor sequence learning progressively re-shapes mu rhythms recorded over premotor regions.

Virtually all studies treat mu trough and peak phases as discrete neurophysiological states. For example, previous work reported that sensorimotor mu trough phases reflect increased M1 neuronal firing rates (Haegens et al., 2011), corticospinal excitability (Bergmann et al., 2019; Hussain et al., 2019; Suresh & Hussain, 2023; Zrenner et al., 2018), inter-hemispheric communication (Stefanou et al., 2018), and enhanced sensitivity to LTP-like plasticity (Baur et al., 2020; Zrenner et al., 2018). In contrast, sensorimotor mu peak phases reflect a relatively quiescent state (Hussain et al., 2019; Suresh & Hussain, 2023; Wischniewski et al., 2022; Zrenner et al., 2018; Haegens et al., 2011; Hussain et al., 2021; Stefanou et al., 2018). Because mu peak and trough phases are in reality continuous components of the same oscillatory cycle, learning-related changes in one phase's physiological properties must also influence other phases (Cole & Voytek, 2017; Jones et al., 2009; Schaworonkow, 2025; Schaworonkow & Nikulin, 2019). Considering this interdependence is especially important when non-invasively evaluating phase-dependent processes outside of M1 by analyzing ongoing cortical activity.

Waveform shape offers a physiologically grounded means of characterizing phase-dependent processes beyond traditional metrics like phase, power, or frequency (Cole & Voytek, 2017). Unlike measurements which rely on external perturbations delivered during specific oscillatory phases (Desideri et al., 2018; Perera et al., 2024; Wischniewski et al., 2025), waveform shape can be extracted from ongoing oscillatory activity without perturbing the underlying system and is therefore a more ecologically valid way to characterize phase-dependent neural processes. Prior work has also repeatedly shown that waveform shape indexes excitation-inhibition balance

(Cole et al., 2017; Cole & Voytek, 2018; Marshall et al., 2022; Opie et al., 2025), reflects circuit-level synaptic interactions (Cole & Voytek, 2018; Jones et al., 2009), and predicts behavior in memory (Trimper et al., 2014), attentional (Opie et al., 2024), and clinical contexts (Cole et al., 2017; Jackson et al., 2019; Szul et al., 2023). Because waveform shape metrics are inherently data-driven, they do not require researchers to arbitrarily pre-define narrow phase ranges *a priori*, nor do they require real-time EEG-informed experimental protocols. Despite these strengths, no studies to date have evaluated the relationship between waveform shape and human motor learning.

To address this gap in knowledge, we characterized mu peak-trough symmetry recorded over left premotor regions before, during, and after healthy adults practiced an implicit serial reaction time task that contained an embedded repeating sequence or no such sequence. As shown previously (Suresh et al., 2025), participants who practiced a version of the SRTT that contained an embedded sequence showed large decreases in sequence-specific reaction times that were retained over time. Although our initial analysis did not identify any learning-related shifts in mu peak-trough symmetry (see Figure 5), a finer-grained analysis focusing on inter-block rest periods showed that mu rhythms became more symmetric with practice. This symmetry increase was significantly stronger for participants in the sequence group than the no-sequence group. Our findings are consistent with the PMC's established role in planning, encoding, and chunking sequence-specific information (Ariani et al., 2025; Diedrichsen & Kornysheva, 2015; Kornysheva & Diedrichsen, 2014), the role of inter-block rest periods in sequence learning (Bönstrup et al., 2019, 2020; Buch et al., 2021; Rumpf et al., 2020), and the importance of wakeful rest in motor learning (Cellini & McDevitt, 2015; Hotermans et al., 2006; Pan & Rickard, 2015). Further, participants who showed the greatest increases in mu peak-trough symmetry also acquired the most sequence-specific skill, with this relationship being stronger for the

sequence than the no-sequence group. Overall, our findings suggest that mu rhythms recorded over premotor regions support the acquisition of sequence-specific skill.

Why might mu rhythms become more symmetric as learning progresses? One possibility is that learning-related increases in mu peak-trough symmetry reflect a redistribution of excitability across the oscillatory cycle that depends on pre-existing mu phase asymmetries. Our data is consistent with this possibility, showing that participants with the largest mu asymmetries at baseline (greatest trough biases) experienced the greatest learning-related increases in mu symmetry (greatest peak shifts). This relationship was quite strong (see Figure 9), suggesting that pre-learning asymmetries and learning-related changes in symmetry rely on the same underlying mechanism. Further, because changes in mu peak-trough symmetry correlated with motor sequence acquisition but not retention, the waveform shape changes observed here likely index plasticity processes involved in the initial formation and encoding of sequence representations. Consistent with this possibility, M1 TMS interventions delivered during sensorimotor mu trough phases elicit LTP-like plasticity (Baur et al., 2020; Zrenner et al., 2018) and boost motor learning (Hussain et al. 2021). Asymmetric, trough-biased mu rhythms may thus provide prolonged windows of opportunity during which the mechanisms supporting sequence encoding are most active. However, learning-related plasticity can increase postsynaptic firing rates (Costa et al., 2004; Kargo & Nitz, 2004), which if not tightly regulated can lead to uncontrolled neural activity. To cope with this challenge, homeostatic mechanisms maintain firing rates within stable limits (Garrido et al., 2016; Turrigiano, 2012). As motor sequence learning progresses, postsynaptic trough-specific firing rates may thus become saturated (Cantarero et al., 2013; Harms et al., 2008). Rather than preventing any additional learning from occurring, task-relevant neurons may instead increase firing rates at other, less excitable mu phases. Such a scenario would effectively redistribute excitability throughout the

mu cycle, resulting in a more symmetrical mu rhythm and decreased phase-specific spiking. This possibility could be tested using invasive recordings that more directly index local neurophysiological properties and is supported by our recent work probing phase-dependent corticospinal plasticity using the same dataset analyzed here (Suresh et al., 2025). In that work, we reported that participants in the no-sequence group showed mu trough-specific corticospinal plasticity while those in the sequence group showed no phase-specific plasticity. We previously interpreted these results as an increase in peak-specific plasticity in the sequence relative to the no-sequence group. However, our current findings instead suggest that sequence learning reduces the neurophysiological differences between mu trough and peak phases, consistent with redistribution of cortical excitability across the mu cycle. Such redistribution would attenuate trough-specific corticospinal plasticity and facilitate peak-specific corticospinal plasticity, consistent with our prior results. In sum, both our prior and current findings suggest that motor sequence learning flexibly redistributes excitability across the mu cycle.

Although the mu rhythm's asymmetric, non-sinusoidal shape was first described more than 70 years ago (Gastaut, 1952; Kuhlman, 1978; Muthukumaraswamy et al., 2004; Pfurtscheller et al., 2006), its role in human sensorimotor control is still poorly understood. The mu rhythm's sharper peaks are thought to result from rapid, synchronous voltage fluctuations in layer V pyramidal neurons driven by changes in the excitatory-inhibitory balance of thalamocortical projections (Buzsáki et al., 2012; Hughes & Crunelli, 2005; Pineda, 2005). Our findings suggest that this asymmetric shape is behaviorally meaningful, such that broader mu troughs may maximize both learning-related increases in mu symmetry and sequence learning itself. Mu rhythm waveform shape could represent a noninvasive marker of motor sequence learning capacity. Yet, although the relationship between waveform shape and learning observed here is mechanistically compelling, it does not establish causality. Transcranial electrical stimulation

(tES) combined with individualized EEG source modeling could be used to experimentally alter mu rhythm waveform shape. For example, asymmetric transcranial alternating current stimulation could feasibly induce a trough-biased mu rhythm in premotor regions prior to sequence learning. Experimentally modifying mu waveform shape in this way could determine its causal role in subsequent sequence learning.

In this study, we provide first evidence that changes in mu waveform shape are associated with human motor learning, but several limitations must be considered. EEG provides excellent temporal, but its spatial resolution is limited. Although we used the Hjorth transformation to improve spatial specificity of the signals analyzed here, we cannot definitively attribute our findings to PMC nor exclude contributions from alternative cortical sources (Schaworonkow & Nikulin, 2019, 2022). Source reconstruction could address this concern, but individual MRIs and digitized electrode locations were not acquired in this study. Relying on a template brain with standard electrode positions can introduce source localization errors of up to ~2 cm (Akalin Acar & Makeig, 2013; Liu et al., 2023), which is the approximate distance between dorsal PMC and M1 (Fink et al., 1997). Template-based source reconstruction would thus not represent a meaningful improvement over the approach used here. To mitigate this limitation, we explored changes in mu-alpha peak-trough symmetry across the scalp. This analysis revealed that mu-alpha peak-trough symmetry increases correlated with sequence acquisition skill only at FC3, our *a priori* region of interest. If this effect was driven by mixing of alternative cortical sources, it should instead be spatially diffuse. Future intracranial recording studies could provide the spatial resolution needed to confirm whether waveform shape changes are specific to PMC.

Additional limitations also exist. Although other complementary waveform shape measures like instantaneous frequency (Quinn et al., 2021a; Quinn et al., 2021b), waveform shape complexity (Parameshwaran et al., 2019) and rise-decay symmetry (Cole & Voytek, 2019; Jackson et al., 2019) exist, we focused solely on mu peak-trough symmetry. These alternative metrics may capture distinct aspects of mu rhythm waveform shape that could further refine our understanding of mu phase-dependent learning mechanisms. The *ByCycle* algorithm requires bandpass filtering, which may increase sinusoidality. However, this would potentially underestimate relationships between waveform shape and learning.

Overall, our findings show that asymmetric, trough-biased mu rhythms recorded over premotor regions become more symmetric during motor sequence learning. Further, the magnitude of premotor mu asymmetry prior to any task exposure and its subsequent re-shaping positively correlates with motor sequence learning. By considering more holistic markers of mu oscillatory activity, our findings provide first evidence that flexible modulation of premotor mu rhythm waveform shape predicts human motor sequence learning.

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Figure 1. Experimental timeline and serial reaction time task (SRTT). A) Experimental timeline. Resting, eyes-open EEG recordings were obtained before (baseline) and at two time points after acquisition (Post0, Post30). SRTT retention was evaluated 1 hour after SRTT acquisition. B) Depiction of implicit SRTT. During SRTT acquisition, participants completed 14 task blocks (120 trials per block). During SRTT retention, participants completed seven blocks (120 trials per block). During sequence blocks (dark gray), the sequence group practiced a version of the SRTT that contained an embedded 12-item sequence. The no-sequence group practiced a version that contained no embedded sequence during any block (all random blocks; light gray). EEG=electroencephalography, SRTT=serial reaction time task.

Figure 2. Group averaged power spectral density estimates recorded at FC3 and the control site. (A and C) Raw power spectral density estimates for the sequence (A) and no-sequence (C) groups prior to any SRTT task performance (i.e., at baseline). (B and D) *Specparam*-modeled power spectral density estimates after subtracting the 1/f aperiodic component for the sequence (B) and no-sequence (D) groups. For all panels, shading reflects the mu-alpha (8-13 Hz) frequency range. Pink=FC3, purple=control/PO4. Note that the y-axis scale for the control site (purple axis) is twice that of FC3 (pink axis) to account for site-specific differences in absolute power.

Figure 3. Cycle-by-cycle analysis of mu rhythm waveform shape. A) Identification of zero-crossings (green), peaks (purple), and troughs (teal) from Hjorth-transformed FC3 mu activity recorded from a representative participant at baseline. B) Filtered Hjorth-transformed mu rhythm recorded from FC3 at baseline. Oscillatory episodes (i.e., bursts) are highlighted in red. C) Visual depiction and calculation of normalized peak-trough symmetry.

Figure 4. SRTT performance. A) Participants in the sequence group showed sequence-specific decreases in mean RTs during acquisition and retention. Vertical dotted lines reflect random blocks (practice block not shown). Blue asterisks reflect significant post hoc pairwise comparisons between blocks 13 and 14 during acquisition and blocks 1 and 2 during retention for the sequence group. Shading represents mean $\pm$ 1 SEM. B) Acquisition and retention skill were both greater for the sequence group than the no-sequence group. For boxplots, black lines represent the median, white dots represent the mean, black dots represent individual participants, and error bars represent the upper and lower interquartile ranges. RT=reaction time; SRTT=serial reaction time task.

Figure 5. No change in mu-alpha peak-trough symmetry after SRTT acquisition. Group-level linear mixed effects model coefficients depicting no changes in mu-alpha peak-trough symmetry for either group following acquisition. Small transparent dots represent individual participant data (blue = sequence; orange = no-sequence), large opaque dots with black edge color represent model coefficients, and error bars reflect 1 SEM. Asterisk reflects main effect of region.

Figure 6. Mu-alpha peak-trough symmetry increases across inter-block rest intervals during SRTT acquisition. Group-level linear mixed effects model estimates depicting changes

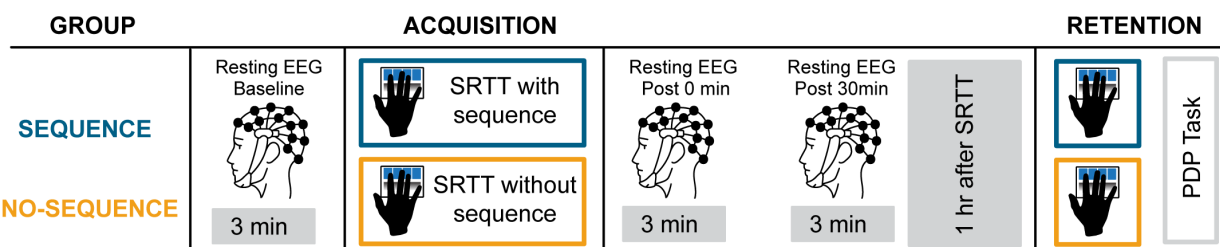
in mu-alpha peak-trough symmetry across rest intervals for FC3 (left) and control (right). FC3 mu peak-trough symmetry increased across rest intervals by shifting towards peak phases; this increase was significantly greater in the sequence than the no-sequence group. Lines reflect model estimates, shading reflects ± 1 SEM.

Figure 7. Changes in FC3 mu waveform shape reflect sequence-specific skill acquisition. Relationship between changes in peak-trough symmetry and acquisition skill for FC3 (A) and the control site (C). This relationship was significantly stronger for the sequence group than the no-sequence group for FC3 but not the control site. Blue text reflects Pearson's correlation coefficient and p-values for the sequence group. Lines reflect model estimates, shading reflects ± 1 SEM.

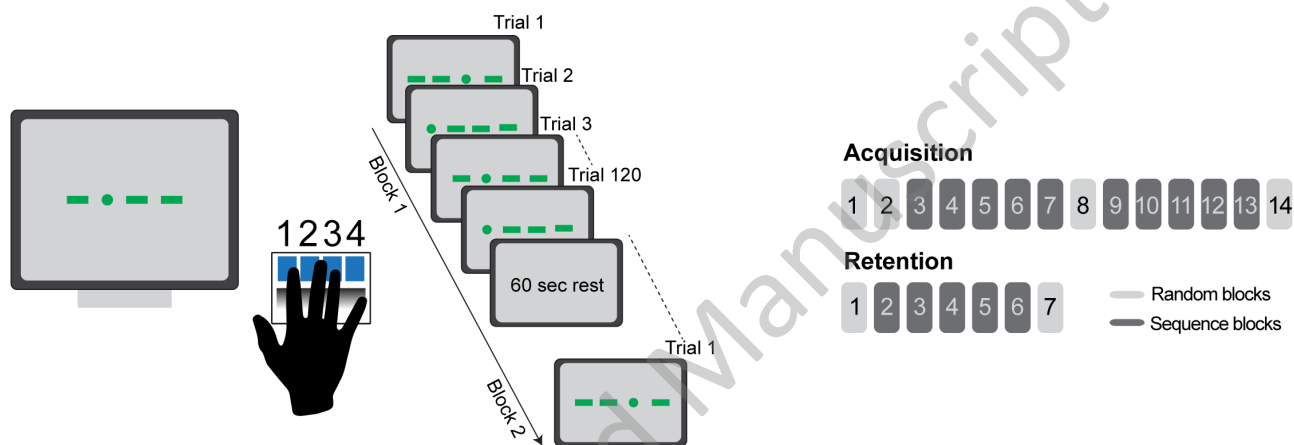
Figure 8. Baseline FC3 mu peak-trough symmetry predicts sequence-specific learning. Relationship between FC3 baseline peak-trough symmetry and acquisition skill. This relationship was significantly stronger for participants in the sequence group than the no-sequence group. Blue text reflects Pearson's correlation coefficient and p-value for the sequence group only. The open circles depict influential observations identified based on Cook's distance (threshold=4/N) representing large baseline FC3 trough bias and acquisition skill in each group. Lines reflect model estimates, shading reflects ± 1 SEM.

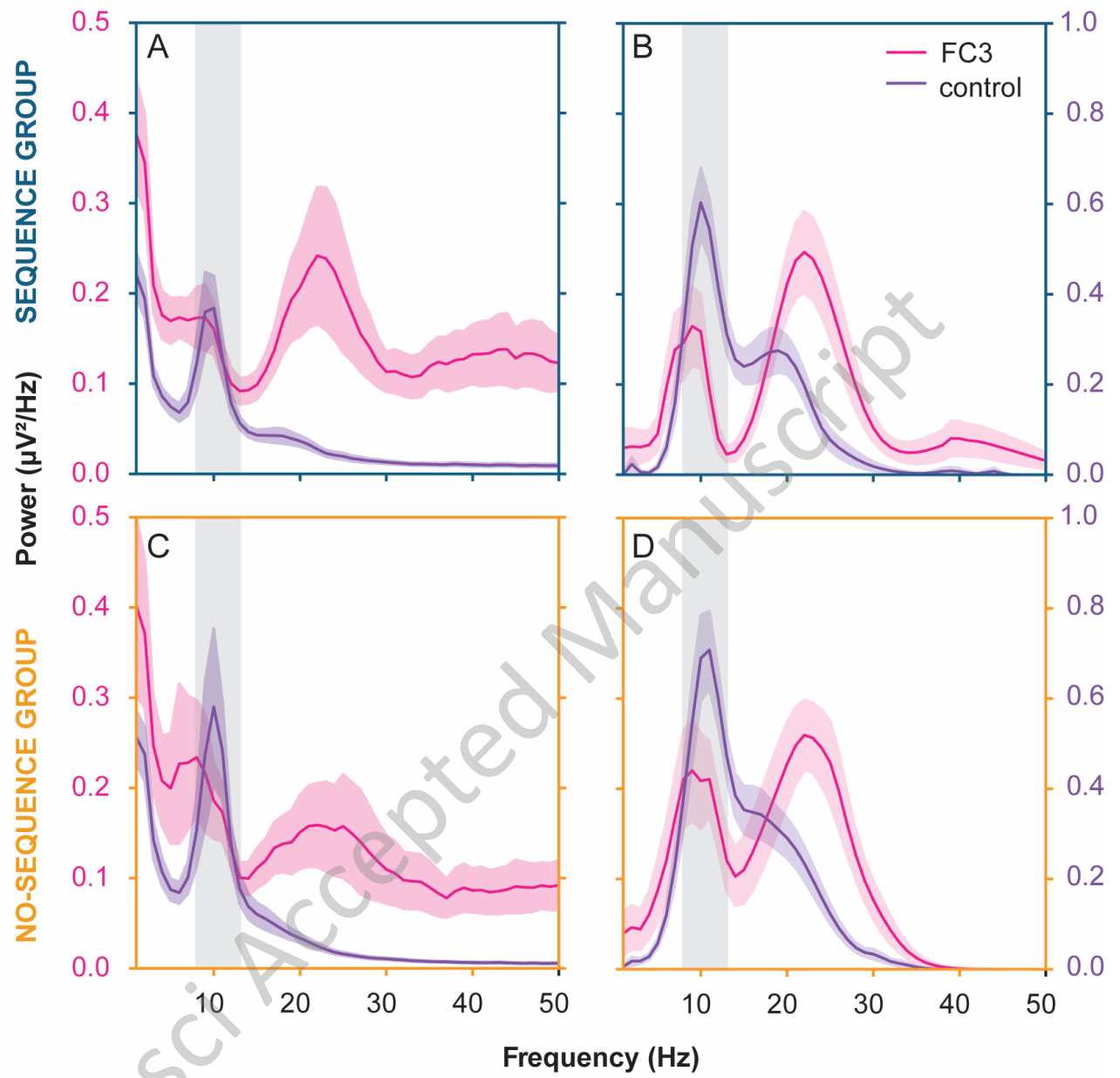
Figure 9. Baseline FC3 mu peak-trough symmetry predicts learning-related symmetry changes. Relationship between FC3 baseline peak-trough symmetry at baseline and after SRTT acquisition in the sequence group. Blue text reflects Pearson's correlation coefficient and corresponding p-value. The open black circles depict influential observations identified based on Cook's distance (threshold=4/N) representing large baseline FC3 trough bias and learning-related FC3 peak shift. Line reflects model estimates, shading reflects ± 1 SEM.

A

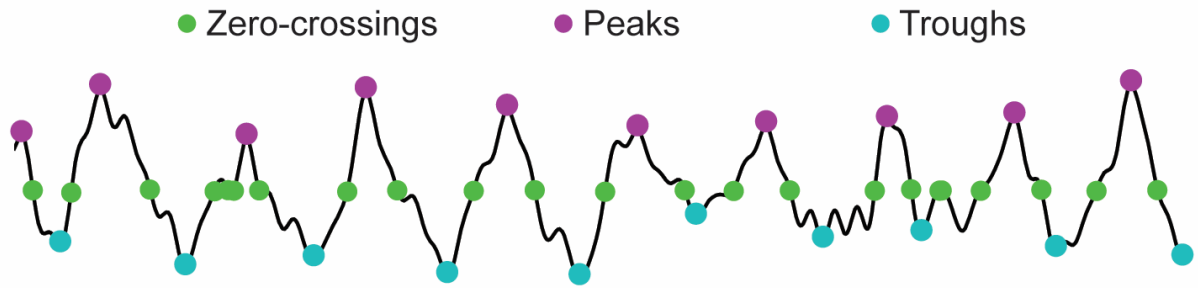


B

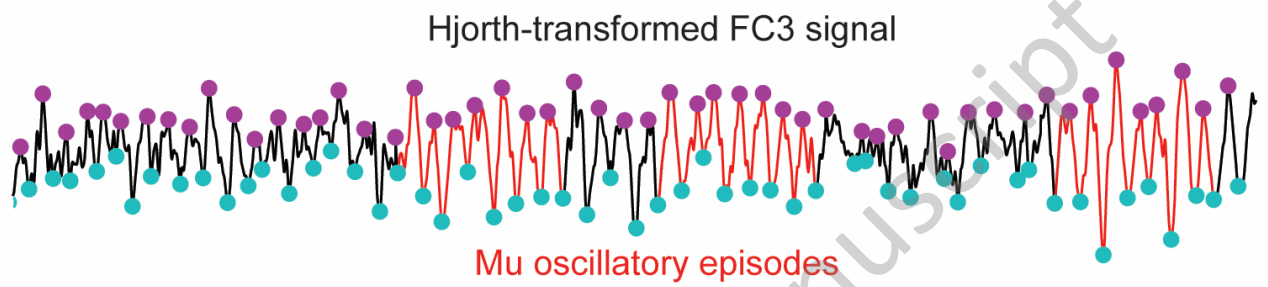




A

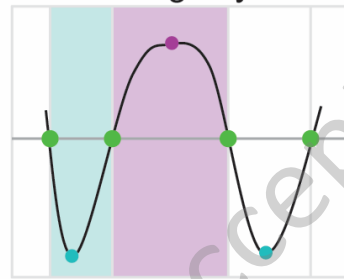


B



C

Peak-trough symmetry



$$= \frac{\text{peak time}}{\text{peak time} + \text{trough time}} - 0.5$$

