# Mu suppression reveals auditory-motor predictions after short motor training in non-musicians

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## ABSTRACT

Auditory-motor coupling is a bidirectional neural mechanism that supports speech and music, as demonstrated by motor system activation during passive listening to learned melodies. Such activation is predictive, occurs in non-musicians after a single motor training session, and can be elicited at the single-note level of the practiced melody. These findings support the idea that motor activity guides auditory perception by relaying predictive timing information. However, the evidence remains incomplete, as the neural processes underlying this anticipatory motor activity are not fully understood. EEG studies in musicians have linked it to mu-band suppression, but the temporal scale at which suppression occurs has not been established, and its generalizability to the broader population remains unclear. To address these gaps, we recruited 25 non-musicians who learned to play a simple melody on a piano-like keyboard. Before and after training, participants passively listened to the trained melody and control melodies. Offline, EEG data from the motor training were used to create a time-frequency mask identifying channels, frequencies, and timepoints likely to display mu suppression during passive listening. Significant mu suppression emerged before each note onset only during post-training exposure to the practiced melody, with no effects in other frequency bands. Results prove that mu suppression occurs at the single-note level following short auditory-motor training and is not dependent on prior musical training. Thus, mu suppression appears tied to the anticipatory motor activity observed in prior studies, supporting the notion that motor activity aids perception by anticipating the unfolding of learned auditory-motor sequences.

## INTRODUCTION

The perception and production of music and speech depend on the integrated representation of sounds and the actions required to produce them. Moreover, the coupling between sound and action is thought to rely on bidirectional information flow between auditory and motor networks (Hickok & Poeppel, 2007; Arnal & Giraud, 2014). Sound-action coupling may be part of innate mechanisms important for learning, or it may be acquired through practice. On the one hand, there is evidence for intrinsic bidirectional interactions between the auditory and motor systems at rest (Bedford et al., 2025) and even in the absence of overt movement (Morillon & Baillet, 2017). On the other hand, there is evidence that these interactions are strengthened by both short- and long-term training (Du & Zatorre, 2017; Herholz & Zatorre, 2012). Regardless, the notion of integrated auditory-motor representations is central to theoretical accounts of sound-action coupling. For instance, the *common coding theory* (Prinz, 1990) and the broader *embodied cognition framework* (Hommel, 2015) maintain that sound-action integration is rooted in overlapping neural codes for both the planning of an action and the representation of its sensory consequences.

The *embodied music cognition* framework as formulated in Maes et al. (2014) proposes that the brain operates on an internal model of the relationship between the body and the environment, which comprises inverse and forward components (Wolpert et al., 1994). Briefly, inverse models enable the prediction of the physical aspects of motion and space implied in the music (Rizzolatti et al., 2001), whereas forward models allow the prediction of the likely auditory outcome of a planned or executed action (Davidson & Wolpert, 2005). Crucially, earlier *embodied music cognition* formulations assumed a passive role for the motor system, relying solely on inverse models to explain the relationship between sounds and actions (Halász & Cunnington, 2012). This initial view was supported by findings that listening to sounds can automatically trigger motor responses based on previously established auditory-motor associations—a phenomenon commonly referred to as *motor resonance*—with neurophysiological and behavioural studies demonstrating faster or more consistent motor activation when sounds and actions had been repeatedly paired (Haueisen & Knösche, 2001; Rusconi et al., 2006).

However, modern *embodied music cognition* accounts recognise that sensory predictions tied to planned actions are routinely projected onto upcoming auditory percepts (Maes et al., 2014), and that predictive models are important for motor control (Hommel, 2015). Specifically, auditory predictions of one's own actions are thought to be responsible for helping the system attenuate, facilitate, and disambiguate the processing of the subsequent self-produced sounds (Maes et al., 2014). Thus, in line with *predictive coding* accounts (Friston et al., 2010), one of the roles of the motor system must be to generate and maintain forward models—whenever auditory-motor associations are available—to streamline auditory processing. For instance, the motor system is now believed to provide top-down predictions about the timing of upcoming auditory events (Patel & Iversen, 2014), a notion that fits into the *predictive timing* framework proposed by Arnal & Giraud (2012). In line with this context, in the current study we trained non-musicians to play a melody and used EEG to measure the note-by-note preparatory motor response during passive listening before and after training. We hypothesized that a larger preparatory response would be observed after training, demonstrating that a predictive auditory-motor representation or forward model had been established through learning (Stephan et al., 2018; Maes et at., 2014).

Evidence for joint auditory-motor representations can be found in neuroimaging and neurostimulation studies showing enhanced activation of motor regions when people listen to melodies they know how to play (Bangert et al., 2006; D'Ausilio et al., 2006; Baumann et al., 2007; Lahav et al., 2007; Lappe et al., 2008; Chen et al., 2012; Herholz et al., 2016). However, none of these studies provide direct evidence that predictable melodic sequences can automatically cue specific upcoming actions. In other words, it is unclear whether this motor activity reflects predictive processes indicative of forward modelling or reactive inverse modelling processes, such as motor resonance. Therefore, in a previous study, we trained non-musicians to play a simple melody and measured motor-evoked potentials (MEPs) to show that hearing the tones of the learned melody automatically activated corresponding motor representations of the associated finger muscles *in advance* of the specific tones (Stephan et al., 2018). This finding is highly suggestive of forward modelling processes, but the MEP is only an indirect measure of motor preparation. Therefore, in the current experiment we used EEG to inspect preparatory motor activity by measuring *mu suppression*—a candidate neural index of forward modelling.

The mu rhythm is a subcomponent of the alpha band typically found between 9-13 Hz (Pineda, 2005) that is thought to reflect the activity of large groups of pyramidal neurons in M1 (Niedermeyer, 1997). This rhythm is characterised by synchronised neural firing at rest, but it desynchronizes quickly in anticipation of voluntary movement, producing a pattern of reduced amplitude known as mu suppression (Pineda, 2005). Another context in which mu suppression has been observed is during the observation of action by others, which inspired mirror neuron (Rizzolatti & Craighero, 2004) and echo neuron (Keysers & Gazzola, 2010) theories, both of which have been implicated in music perception (Overy & Molnar-Szakacs, 2009). However, mu suppression is not limited to anticipating active self-movement or when observing movement by others; it also emerges during passive listening to sounds produced by familiar actions, lateralizing to the contralateral hemisphere at effector-specific locations within sensorimotor cortex (Pineda et al., 2013). This suggests that mu suppression may index predictive action-perception coupling more broadly (Pineda, 2005).

For instance, Wu et al. (2016) reported mu suppression in expert pianists during passive listening to a practiced melody, but not to unfamiliar melodies. This effect preceded the onset of each practiced melody presentation, suggesting that mu suppression may indeed reflect covert motor activity that supports forward modelling. However, because mu suppression was only measured per melody and not in relation to each note in the melody, this study could not demonstrate effector-specific predictions driven by the learned sequence rather than general expectancy (Novembre & Keller, 2014). Moreover, because only musicians were tested, the study could not determine whether the observed mu suppression was the result of global predictions contingent on prior musical training or whether it was directly linked to learned auditory-motor associations.

In light of these gaps, in the current study we used the same melody learning task as in our previous MEP study, combined with EEG, to measure possible changes in mu suppression following short-term training in non-musicians. In this task, participants passively listened to learned and unlearned melodies before and after 15 blocks of training on the learned melody. We then compared mu activity preceding each note, with the hypothesis that mu suppression for the learned melody would be greater than for unlearned melodies before each note. To objectively identify the likely time-frequency distribution of mu suppression during the passive listening task, we used the EEG data collected during active motor training to derive a time-frequency mask of all frequency bands engaged by the task. We then applied this mask to the passive listening data, which allowed us to assess the pattern of change across all active frequency bands, as well as to test whether any observed suppression effects would be specific to the mu frequency band.

## METHODS

### Participants

We recruited 27, healthy, right-handed non-musicians. Two participants were excluded due to poor EEG data quality, resulting in a final sample of 25 participants (14 females) aged between 18 and 35 years (mean = 22.6 ± 4.5 years). Consistent with previous studies, all participants had less than 3 years of lifetime musical training and/or experience and reported no active music-making within the 3 years prior to the study (Slater & Kraus, 2016). Exclusion criteria included left-handedness and a history of psychiatric or neurological disorders. All participants provided written informed consent at the start of the experimental session. The study protocol adhered to the principles of the Declaration of Helsinki (World Medical Association, 2001) and was approved by the McGill Human Research Ethics Board.

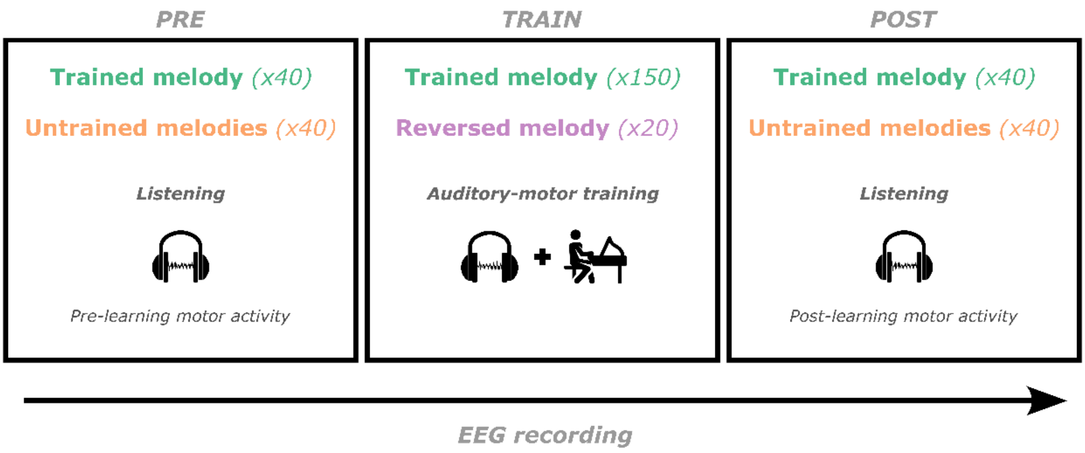
### Task and stimuli

The goal of the experiment was to assess the degree of mu suppression during passive listening to a trained melody. EEG was recorded throughout the experiment, which featured three conditions summarized in Figure 1A: pre-training passive listening (PRE); melody playback training (TRAIN); and post-training passive listening (POST). In the PRE and POST conditions participants heard two types of melodies: 1) the trained melody (Trained); and 2) untrained melodies (Untrained). In the TRAIN condition participants either listened to and played back to blocks containing repetitions of the Trained melody or catch blocks containing repetitions of the reversed Trained melody (Reversed).

41 unique 8-note melodies (1 trained melody and 40 control melodies) were created using the four notes in a C-major arpeggio that corresponded to the four digits of the right hand when played back on a purpose-built piano-like keyboard (C4 (259 Hz) = index; E4 (329 Hz) = middle; G4 (389 Hz) = ring; C5 (531 Hz) = pinkie). Melodies were 12 seconds long, with each note lasting 600 milliseconds, followed by an inter-stimulus interval of 900 milliseconds, resulting in an onset-to-onset asynchrony of 1500 milliseconds. Moreover, melodies were constructed such that

each note appeared twice and no notes were repeated sequentially (Stephan et al., 2018). The Trained melody is depicted in Figure 1B. All sounds were delivered via E-A-RTONE 3A foam-tipped insert-type earbuds (E-A-R® Auditory Systems). Sounds were synthesized with Adobe® Audition v.3.0 (Adobe Systems Incorporated, 2007); all musical notes were rendered using a piano timber, and every melody presentation in the TRAIN condition was cued by a woodblock sound.

A) **Study design**


PRE
TRAIN
POST
Trained melody (x40)
Untrained melodies (x40)
Listening
Pre-learning motor activity
Trained melody (x150)
Reversed melody (x20)
Auditory-motor training
Trained melody (x40)
Untrained melodies (x40)
Listening
Post-learning motor activity
EEG recording

B) **Trained melody**

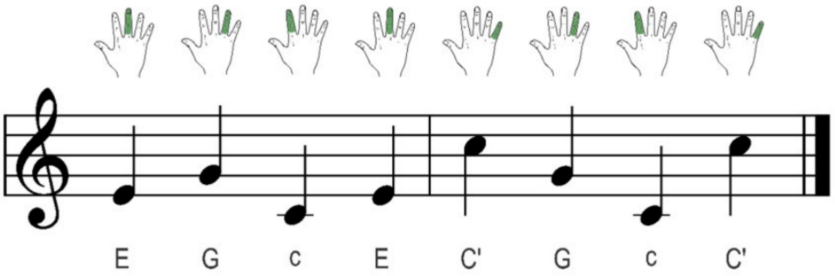


**Figure 1.** **Experimental paradigm.**

**A)** Study design. **PRE (panel 1)**: subjects passively listened to one block of 40 repetitions of the Trained melody and one block of 40 Untrained melodies. **TRAIN (panel 2)**: subjects listened to and played back to 15 blocks of 10 repetitions of the Trained melody and two catch blocks of 10 repetitions of the Reversed melody. **POST (panel 3)**: identical to PRE. **B)** Trained melody. The arrangement is based on a C-major arpeggio. Each note is associated with one digit of the right hand. The sequence has isochronous timing.

PRE and POST passive listening conditions

During the PRE and POST passive listening conditions, participants listened to one block of 40 repetitions of the Trained melody and one block of 40 unique Untrained melodies (12.7 minutes per block). As an attentional control, seven catch melodies were presented across the two blocks of each passive listening condition (PRE and POST), in which the last note was mistuned [C#5 (554 Hz) instead of the natural C5 (531 Hz)]. Participants were instructed to silently count these mistuned notes and report the total at the end of each block. The presentation order of the Trained and Untrained blocks was held across passive listening conditions PRE and POST but counter-balanced between participants. Inter-trial intervals (ITIs) for melodies presented in the passive listening blocks varied randomly between a 3.3 and 3.7 second range (in 0.1 second steps) to prevent anticipation of melody onsets.

Melody playback training (TRAIN)

The TRAIN condition consisted of 15 blocks (10 trials each) of practice on the Trained melody and 2 catch blocks (10 trials each) of practice on the Reversed melody, for a total of 17 blocks (~50 minutes of training). Reversed melody blocks appeared in the 3rd and 15th block positions. The ITI within all blocks was fixed at 3.5 seconds. On each trial, participants heard a given melody and were asked to reproduce the notes by pressing four keys on a purpose-built piano-like keyboard. Notes produced by participants' key presses were played back at an octave below the original melody to provide distinguishable auditory feedback. Participants were instructed to synchronize their responses as closely as possible to each melody presentation, and no additional instructions or performance feedback were provided.

Each keypress activated a switch on the custom keyboard that sent transistor-transistor logic pulses via a parallel port connected to a Beaglebone® Black microcomputer equipped with a Bela real-time module (Thangaraj, 2016), based on the system introduced by Zappi & McPherson (2014). These pulses were received by the EEG recording computer with minimal delay and low jitter and were used as precise event markers for keypress timing.

### Behavioural data analysis

Individual performance in the motor training task (TRAIN) was evaluated for each of the 17 blocks using two metrics: the percentage of correct key presses (accuracy) and the mean absolute timing difference between key presses and target note onsets (reaction time). A key press was considered accurate if it matched the pitch of the intended note within a ±300 millisecond window and was executed without overlapping with other key presses. Reaction times (RTs) were computed only for correct key presses. In cases where individual RTs were missing in a trial within a block, values were imputed using the mean RT for that block's trial, calculated across all other participants.

### EEG data collection

EEG recordings were collected using a 64-channel active electrode cap (actiCAP, Brain Products GmbH, Gilching, Germany), a unipolar EEG amplifier (BrainAmp, Brain Products GmbH, Gilching, Germany), and dedicated recording software (BrainVision Recorder, Version 1.20.0801, Brain Products GmbH, Gilching, Germany, 2019), all from the same manufacturer. Data were sampled at 1 kHz. The ground electrode was left at the default FPz location, and the reference electrode was placed on the right canthus to monitor eye blinks. Cap electrodes were arranged at 60 standard positions according to the international 10-10 system (Chatrian et al., 1988).

Electrodes corresponding to channels FT9 and FT10 were placed on the left outer canthus and right cheek, respectively, to capture horizontal and vertical electrooculography (EOG) signals used to monitor blinks and saccadic eye movements. Electrodes corresponding to channels TP9 and TP10 were placed on the left and right mastoids, respectively, and served as re-reference sites for offline data preprocessing. Throughout the EEG recording, participants were instructed to maintain their gaze on an onscreen central fixation cross. Impedance levels were checked at the end of each passive listening block in the PRE and POST conditions, as well as midway through the TRAIN condition, and were continuously maintained below 10 kΩ. During passive listening, participants were instructed to remain as still as possible, and their right hand was monitored to ensure that no movements contaminated the EEG recording.

EEG pre-processing

EEG data were pre-processed using a combination of Brainstorm (Tadel et al., 2011) custom scripts in MATLAB R2021a (version 9.10.0; The MathWorks Inc., 2022), following standard preprocessing and artifact removal steps: EEG signals were notch-filtered at 60 Hz, bandpass-filtered between 1-100 Hz, and re-referenced to bilateral mastoids. Noisy segments and channels were identified and removed through visual inspection (Gross et al., 2013). To assist in removing artifacts and bad channels, power spectrum density (PSD) plots were generated at successive stages of pre-processing. Across all participants, a total of 29 faulty channels were interpolated across 11 participants, with no more than 8 interpolations for any given participant (mean = 2.64 ± 2.11 channels). Repetitive eye blink artifacts were removed for all subjects using Brainstorm's built-in signal space projection method (Tesche et al., 1995), and saccade artifacts were removed in three participants using the same method.

EEG data analysis

*Time-frequency analysis*

After preprocessing, the EEG data corresponding to the PRE and POST passive listening conditions were downsampled to 200 Hz, epoched from -2000 to 2000 milliseconds relative to each individual note's onset, and baseline-corrected from -1245 to 1245 milliseconds to account for the approximately ± 200 milliseconds of edge artifacts introduced by subsequent wavelet convolution. This procedure yielded 320 epochs per participant and listening block (40 melodies × 4 unique notes per melody × 2 unique note repetitions per melody). To isolate induced activity, the average event-related potential for each participant and listening block was subtracted from individual EEG epochs, under the notion that any effects occurring prior to note onset can only be induced rather than evoked (Cohen, 2014).

Epochs were then convolved over a linearly scaled frequency range of 2-49.5 Hz (step size: 0.5 Hz) using a family of Gaussian-tapered scaling Morlet wavelets with the mother wavelet centred at 1 Hz and an initial full-width at half maximum of 3 seconds. This approach yielded time-frequency power estimates, which were subsequently normalized using Brainstorm's event-related spectral perturbation (ERSP) baseline correction method (Tadel et al., 2011). The baseline window was set from −850 to −650 milliseconds relative to note onset, corresponding to the midpoint (750 milliseconds) ±100 milliseconds between successive notes, where motor activity was expected to be minimal.

The 320 time-frequency plots were averaged within each passive listening block for each participant, yielding four averaged time-frequency plots per participant comprising the mean activity across all four fingers. The final plots contained baseline-corrected power estimate values across 64 channels, 97 frequency bins spanning 2 to 49.5 Hz, and 801 timepoints (sampled at 200 Hz).

*Time-frequency mask*

To examine changes in EEG activity during listening in the PRE and POST conditions we wanted to independently identify the predicted distribution of possible effects across channels, time and frequency. To this end, we computed a group-level, time-frequency mask based on correctly performed trials of individual key presses in the TRAIN condition, across all frequency bands within the 2-49.5 Hz range, in the time window expected to be associated with response preparation (−650 to −100 milliseconds before note onset). The purpose of this mask was to identify channels, frequencies, and timepoints most likely to exhibit mu suppression during post-training passive listening to the Trained melody. In other words, our mask was defined from independent data to avoid circularity (Kriegeskorte et al., 2009), in line with standard practice and recommendations (Maris & Oostenvelt, 2007).

For each participant, we selected the four blocks from blocks 9-17 (excluding catch block 15) of the TRAIN condition with the highest average accuracy scores. From these, a total of 320 epochs were extracted per participant (10 melodies × 8 notes per melody × 4 Trained melody blocks), and time-frequency decomposition was performed on each epoch using the same epoching procedure, time-frequency parameters, and ERSP baseline-correction method described above. Each resulting plot contained baseline-corrected power estimate values across 64 channels, 97 frequency bins spanning 2 to 49.5 Hz, and 801 timepoints (sampled at 200 Hz). All 320 time-frequency plots were then averaged at the participant level, yielding one average time-frequency plot per participant comprising the mean activity across all four fingers, for a total of 25 participant-level plots.

The 25 active motor training time-frequency plots were compared against zero using a one-sample, left-tailed *t*-test. For this test, only the 111 timepoints ranging from −650 to −100 milliseconds relative to note onset were selected in order to isolate a time window likely to contain preparatory auditory-motor activity (Shibasaki & Hallet, 2006). The window was truncated at −100 milliseconds to avoid contamination from auditory (Ross et al., 2022) and movement activity (Frølich et al., 2018) occurring close to note onset.

The resulting *t*-map was submitted to a cluster-based permutation test implemented via FieldTrip's native `ft_freqstatistics` function within Brainstorm (Oostenveld et al., 2011; Tadel et al., 2011). To control for multiple comparisons, the test was configured to run 1000 Monte Carlo permutations (Candia-Rivera & Valenza, 2022; Pernet et al., 2015). The significance threshold for both the *t*-test and the permutation test was set at the standard alpha level of .05 ($p$ = .05). No averaging was performed across dimensions. Regions of interest (ROIs) were allowed to vary freely across time and frequency, provided that activity maintained contiguity within a cluster, defined as at least one time-frequency pixel connected across at least two channels.

The resulting cluster-corrected *t*-map was thresholded to retain only pixels with an associated *p*-value less than .05. This thresholded t-map served as a binary mask, whereby all surviving pixels were weighted equally when applied to the passive data, regardless of their associated *t*-statistic value.

The significant cluster was then divided into three frequency bands: mu (9-16.5 Hz), beta (16.5-33.5 Hz), and gamma (33.5-49.5 Hz). The beta-gamma division was determined based on prior literature, as significant activity between 17 and 49.5 Hz was spectrally contiguous across all 60 channels. In contrast, the mu-band boundaries were determined empirically: among the 33 channels showing significant activity between 9 and 16.5 Hz, 29 displayed mu-band activity that was clearly separated from beta-band activity by several frequency bins containing no significant pixels (see Fig. 3B, channel C3, for an example). In the remaining four channels (C5, CP5, T7, TP7), a small amount of intervening activity bridged the mu and beta ranges. This bridging likely caused pixels in the mu range to be included in the same statistical cluster as those in the beta-gamma range. However, the intervening activity was temporally restricted, and the overall time-frequency profile still matched the isolated mu-band patches observed in the other 29 channels. Thus, we believe our mu-beta partition to be sufficiently grounded.

After defining the mu-beta-gamma partitions, we applied the mask to the passive listening data in order to extract band-specific power estimates. For each participant and passive listening block, all nonzero baseline-corrected power values (representing the difference between signal power and the time-frequency baseline at each pixel) were averaged across the pixels that survived thresholding within each frequency band separately, collapsing across all channels that displayed activity in that band and across all 111 timepoints spanning −650 to −100 milliseconds relative to note onset. This procedure yielded one scalar value per participant, per frequency band, and per passive listening block to be used in subsequent statistical analyses.

## Statistical analyses

### *Behavioural performance (TRAIN)*

A Generalized Linear Mixed Model (GLMM) approach was used for all statistical analyses involving behavioural measures, due to the non-normal distribution of the data and this method's capacity to account for random effects associated with individual differences (Stroup, 2012). All GLMM analyses were conducted using the `glmmTMB` package (Brooks et al., 2017) in RStudio version 2022.02.0 (Posit team, 2022).

Two sets of statistical analyses were performed to verify that participants had successfully learned the Trained melody sequence. The first analysis tested for learning across the 15 Trained melody blocks using a one-factor, within-subjects design in two separate GLMMs: one with accuracy and the other with reaction time as the dependent variable. In both models, block was included as a fixed within-subjects factor. The same block factor was incorporated into the random effects structure—allowing for random slopes and intercepts—with subject ID set as the grouping variable (1 + block || subject).

The second analysis tested for sequence-specific learning using a two-factor, within-subjects design across two additional GLMMs: one for accuracy and one for reaction time. These analyses compared average performance for Trained melody blocks 2 and 14 to the two Reversed melody blocks (3 and 15). Each GLMM included condition (Trained vs. Reversed) and block (start vs. end of training) as fixed within-subjects factors, along with their interaction term (condition × block). The same two factors were included in the random effects structure to allow for random slopes and intercepts, and subject ID was set as the grouping variable (1 + condition + block || subject).

Accuracy data exhibited a bimodal, non-normal distribution. As such, percentage scores were converted to proportions and modelled using a beta distribution with a logit link function. Reaction time data closely followed a gamma distribution, as expected for response latency measures (McGill & Gibbon, 1965), and were therefore modelled using a gamma distribution with an inverse link function. Across GLMMs, omnibus tests were evaluated using *F* statistics, and FDR-corrected *t*-statistics were computed from two-tailed, paired-sample *t*-tests on the prediction scale. Resulting metrics were back-transformed to the response scale. Degrees of freedom were specified as the residual degrees of freedom at the observation level.

*EEG activity during passive listening (PRE and POST)*

To test whether EEG activity would exhibit the predicted mu suppression exclusively during post-training passive listening to the Trained melody, we performed left-tailed, one-sample, *t*-tests against zero on the 25 average baseline-corrected power estimate values, separately for each of the four passive listening blocks, within each of the three frequency bands. As a total of 12 tests were conducted (4 passive listening blocks × 3 frequency bands), significance was corrected for multiple comparisons using non-parametric permutation testing with 10,000 iterations.

We further tested for factorial interactions by implementing three GLMMs, one for each frequency band. Specifically, we used a 2×2 within-subjects design with condition (Trained vs. Untrained) and time (Pre- vs. Post-training) as fixed effect factors, along with their interaction term (condition × time). The same two factors were included in the random effects structure, which allowed for random slopes and intercepts, with subject used as the grouping variable (1 + condition + time || subject). The dependent variable in each model was the 25 channel-averaged, baseline-corrected power estimate values in each of the four passive listening blocks. The dependent variable was modeled using a Gaussian distribution, as differential values resulting from baseline correction operations are expected to approximate normality (Field, 2013).

Omnibus tests were computed from the model using *F* statistics, and uncorrected *t*-statistics were derived from two-tailed, paired-sample *t*-tests conducted directly on the response scale. Degrees of freedom at the observation level were defined by the model's residual degrees of freedom. Because this GLMM structure was applied across three frequency bands, significant *t*-statistics were corrected for multiple comparisons using non-parametric permutation testing (10,000 iterations).

Finally, we assessed relative pre-post changes between Trained and Untrained melodies. This approach explicitly accounted for differences in post-training values relative to baseline pre-training values, which may have been obscured when examining absolute changes under a factorial design. For each frequency band, relative change scores were calculated by subtracting pre-training baseline-corrected power estimate values from post-training values and scaling the result by the absolute value of the former. Given the expected presence of outliers resulting from this type of ratio-based calculation, statistical comparisons were conducted using a non-parametric Wilcoxon signed-rank exact test. Moreover, as these tests were conducted across three frequency bands, significance levels were corrected for multiple comparisons using non-parametric permutation testing (10,000 iterations).

### *Brain-behaviour correlations*

To assess whether individual differences in motor learning in the TRAIN condition were associated with changes in brain activity in the PRE and POST passive listening conditions, we conducted four Spearman rank-order correlation tests. The degree of motor learning was quantified by computing the slope of change in average accuracy and RTs across Trained melody blocks 4-14 of the motor training task. Individual accuracy and RT slopes were then correlated with individual scores in two EEG-derived measures within the mu frequency band: (1) baseline-corrected power estimate values during passive listening to the Trained melody in the post-training block, representing *absolute* mu suppression activity; and (2) the normalized pre-post difference between Trained and Untrained melodies, representing *relative* mu suppression activity after training with respect to before training. Spearman's rank-order method was used due to the presence of non-normality and potential outliers in the data.

## RESULTS

### Attentional control task

As an attentional control 7 mistuned notes were presented during each of the PRE and POST passive listening conditions. Across both conditions, participants reported an average 10.44 and 7.52 mistuned notes, indicating that they were actively engaged in listening during the passive task.

### Behavioural performance

We tested for a main effect of motor learning across blocks of training. For accuracy, we observed a significant effect of block ($F(14, 344) = 47.53$, $p < .001$), indicating a global increase in accuracy as training progressed (Figure 2A). For RT, we similarly observed a significant main effect of block ($F(14, 344) = 19.96$, $p < .001$), indicating a concomitant global decrease in reaction times over the course of training.

Next, we tested for sequence-specific learning by comparing Trained melody blocks 2 and 14 to Reversed melody blocks 3 and 15. For accuracy, we observed a significant main effect of both condition ($F(1, 92) = 48.4$, $p < .001$)—such that accuracy was greater for Trained than Reversed melodies throughout training—and block ($F(1, 92) = 28.05$, $p < .001$), such that accuracy increased from Start to End of training across both melody types. We also obtained a significant interaction term ($F(1, 92) = 12.8$, $p < .001$), such that the start-to-end increases in performance were comparably greater for Trained melodies than Reversed melodies, as revealed by a second-order interaction test ($t(92) = 4.72$, $p < .001$).

For RT, we similarly observed significant main effects for both block ($F(1, 92) = 22.77$, $p < .001$)—indicating shorter RTs throughout training to the Trained melody compared to the Reversed melody ($t(92) = −4.66$, FDR-corrected $p < .001$)— and time ($F(1, 92) = 39.1$, $p < .001$), indicating shorter RTs at the End compared to the Start of training for both melody types ($t(92) = −5.79$, FDR-corrected $p < .001$). The interaction term was not statistically significant ($F(1, 92) = 0.9$, $p = .34$). Together, these results indicate that participants learned the specific Trained melody sequence well.

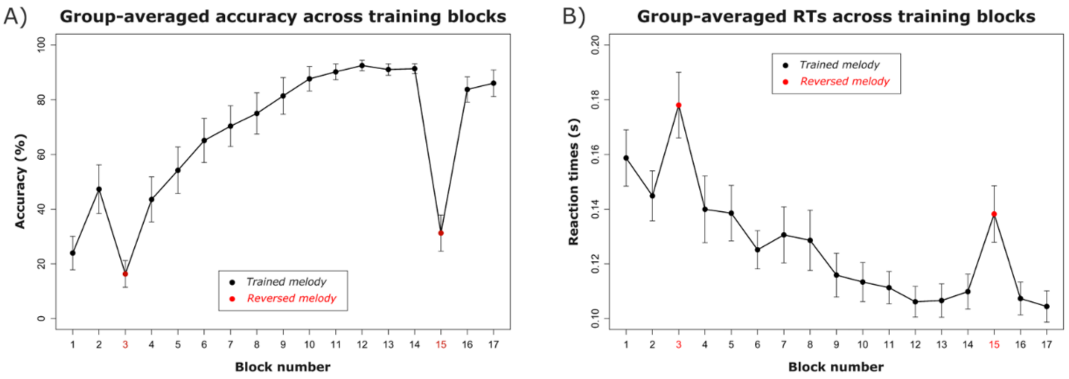


**Figure 2.** **Behavioural performance scores of the TRAIN condition.**
**A)** Group-averaged accuracy across training blocks. Overall accuracy scores improved throughout the TRAIN condition. Reversed melody blocks 3 and 15 exhibit a significant drop in performance compared to Trained melody blocks 2 and 14, indicating sequence-specific learning of the Trained melody. **B)** Group-averaged RTs across training blocks. Overall reaction times diminished throughout the TRAIN condition. Reversed melody blocks 3 and 15 exhibit a significant increase in latency compared to Trained melody blocks 2 and 14, indicating sequence-specific learning of the Trained melody.

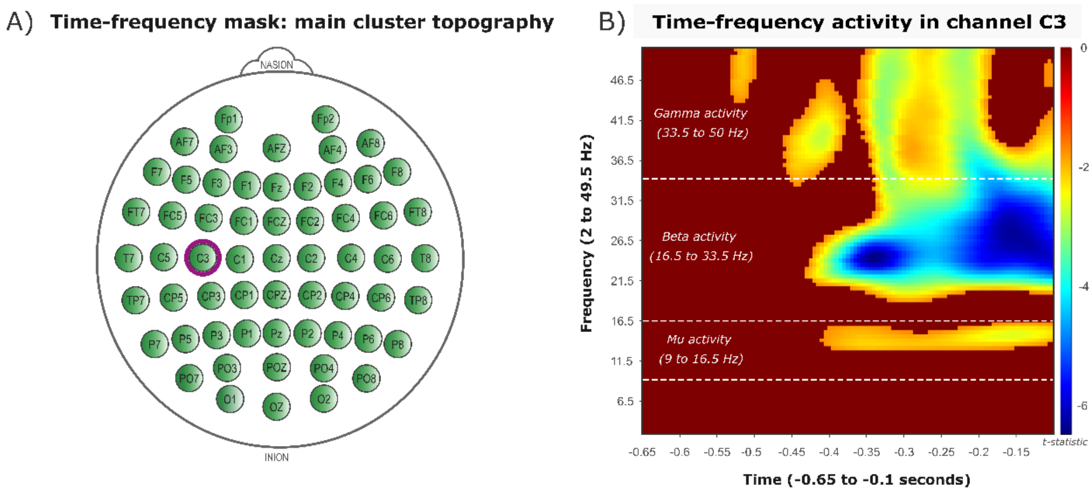
## Brain activity

### *Time-frequency mask*

The cluster permutation test yielded a time-frequency *t*-map (Figure 3A) comprising 60 channels, 97 frequency bins, and 111 timepoints (sampled at 200 Hz). Channel FPz had been used as ground, and channels FT9, FT10, TP9, and TP10 had been used as external electrodes, so all five were excluded from the test.

The time-frequency *t*-map comprised one significant *channel* × *frequency* × *time* cluster (1,000 permutations, *p* = .001). The cluster (cluster-level statistic [maxsum] = −725,558; size = 238,299 pixels) encompassed all 60 channels, spanned frequencies specifically from 9 to 49.5 Hz, and featured activity across the entire time window ranging from −650 to −100 milliseconds. Within this cluster, we examined three frequency bands: mu (9-16.5 Hz; 33 channels), beta (16.5-33.5 Hz; 60 channels), and gamma (33.5-49.5 Hz; 60 channels; Figure 3B).

The activity in the mu frequency band resulting from the cluster permutation test was interpreted as reflecting true, active mu suppression prior to note onset, based on its distinct, spectrally and spatially confined location within the cluster (Figure 4A). Namely, this activity was restricted to a reduced subset of 33 channels—29 of which were spectrally isolated from the beta band (see Figure 3B for an example in C3)—and was left-lateralized, as expected for a right-hand response.


A) Time-frequency mask: main cluster topography

B) Time-frequency activity in channel C3

**Figure 3.** **Results of the time-frequency mask derived from the TRAIN condition.**

**A)** Topography of the time-frequency mask. **Green** indicates channels that survived the cluster-permutation test (n = 60). Channel C3 is highlighted in purple. **B)** Spectrotemporal distribution of the time-frequency mask in channel C3. Coloured pixels are those that survived standard thresholding ($p < .05$). The colour coding indexes the t-statistic at each pixel. Surviving pixels were masked equally onto the passive data in binary fashion, regardless of *t*-statistic value. The cluster activity was further divided into **mu** (9-16.5 Hz), **beta** (16.5-33.5 Hz), and **gamma** (33.5-49.5 Hz) frequency bands. The spectral and temporal distribution of the surviving pixels in these frequency bands varied slightly across channels.

### *EEG activity during passive listening blocks*

To test the presence of suppression across the four passive listening blocks, we conducted a series of 12 left-tailed, one-sample *t*-tests against zero (Figure 4B; Table 1) across the mu, beta and gamma frequency bands. Results revealed significant suppression relative to baseline only within the pixels representing activity in the mu frequency band, and only during post-training passive listening to the Trained melody ($t(24) = -2.4$, permutation-corrected $p = .01$).

**Table 1.** Left-tailed, one-sample *t*-tests against zero

| ROI | Group 1 | Group 2 | *n* | *t*-statistic | *df* | *p*-value |
|---|---|---|---|---|---|---|
| **Mu** | Target melody PRE training | null model | 25 | -1.3 | 24 | .10 |
| | Scrambled melodies PRE training | null model | 25 | 1.32 | 24 | .90 |
| | Target melody POST training | null model | 25 | -2.4 | 24 | **.01*** |
| | Scrambled melodies POST training | null model | 25 | -0.57 | 24 | .29 |
| **Beta** | Target melody PRE training | null model | 25 | -0.46 | 24 | .32 |
| | Scrambled melodies PRE training | null model | 25 | 1.07 | 24 | .85 |
| | Target melody POST training | null model | 25 | -0.5 | 24 | .30 |
| | Scrambled melodies POST training | null model | 25 | 0.45 | 24 | .67 |
| **Gamma** | Target melody PRE training | null model | 25 | -1.34 | 24 | .10 |
| | Scrambled melodies PRE training | null model | 25 | 1.41 | 24 | .91 |
| | Target melody POST training | null model | 25 | -1.24 | 24 | .11 |
| | Scrambled melodies POST training | null model | 25 | -0.19 | 24 | .42 |

Within the mu frequency band, GLMM results additionally revealed a significant main effect of condition (*F*(1, 92) = 5.2, *p* = .02). A subsequent post hoc test indicated that the change in power with respect to time-frequency baseline (baseline-corrected power estimate values) for the Trained melody was negative and greater than for the Untrained melodies (*t*(92) = −1.92, permutation-corrected *p* = .047). Neither the main effect of time (*F*(1, 92) = 3.18, *p* = .08) nor the interaction term (*F*(1, 92) = 0.03, *p* = .87) reached significance.

By contrast, the same GLMM structure revealed no significant main effects or interactions within the beta frequency band (condition: *F*(1, 92) = 1, *p* = .32; time: *F*(1, 92) = 0.03, *p* = .87; condition × time: *F*(1, 92) = 0, *p* = .95), nor within the gamma frequency band (condition: *F*(1, 92) = 2.38, *p* = .13; time: *F*(1, 92) = 0.67, *p* = .41; condition × time: *F*(1, 92) = 0.6, *p* = .44).

To further test whether passive mu suppression was greater in response to the Trained melody following motor learning, we assessed the relative pre-post change in activity. The Wilcoxon signed-rank exact test revealed significantly greater normalized pre-post mu suppression for the Trained melody compared to the Untrained melodies (Figure 4C; *V* = 97, permutation-corrected *p* = .04).

Conversely, no significant differences were observed in the beta frequency band (*V* = 140, *p* = .28) or in the gamma frequency band (*V* = 217, *p* = .93). These findings confirm that, when explicitly accounting for pre-post differences, a significant relative suppression emerges for the Trained melody only within the mu frequency band, thereby complementing and extending the results of the one-sample *t*-tests against zero and the factorial design.

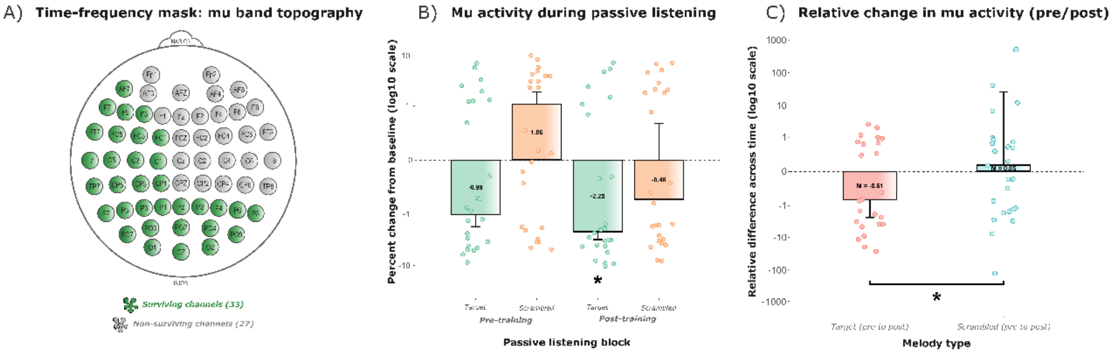


**Figure 4.** **Mu band activity across PRE and POST conditions.**

**A)** Topography of the mu frequency band. **Green** indicates channels in the cluster that display mu activity (n = 33). **Grey** indicates the channels in the cluster that do not display any mu activity (n = 27). **B)** Subject-averaged mu activity within each passive listening block. Baseline-corrected power estimate values representing the difference between signal power and baseline in each pixel of the mu frequency band were averaged across channels within each passive listening condition, for each subject. The post-training Trained melody block was the only block that displayed significant group-level suppression with respect to zero in the mu frequency band. Data are presented in a logarithmic scale for display purposes. **C)** Relative pre-post change in mu activity for Trained vs Untrained melodies. Relative change scores were computed by subtracting pre-training baseline-corrected power estimate values from post-training values and dividing by the absolute value of the former. The Trained melody exhibited significantly greater median suppression across time compared to the Untrained melodies. Data are presented in a logarithmic scale for display purposes.

### *Brain-behaviour correlations*

To test for a relationship between individual differences in learning and mu suppression, we correlated one absolute measure and one relative measure of mu suppression with the slopes representing change in accuracy and RT during motor training. Neither correlation between the accuracy slope and the two measures of brain activity were statistically significant (post-training Trained melody values: $\rho$ = .25, *p* = .23; relative pre-post difference between Trained and Untrained melody types: $\rho$ = −.04, *p* = .85). Equally, neither correlation between the RT slope and the two measures of brain activity were statistically significant (post-training Trained melody values: $\rho$ = .03, *p* = .89; relative pre-post difference between Trained and Untrained melody types: $\rho$ = −.27, *p* = .19).

## DISCUSSION

The goal of this study was to assess the learning of new auditory-motor representations by quantifying the degree of anticipatory mu suppression occurring at the single-note level during passive listening to trained versus untrained melodies. To test these ideas, we generated a time-frequency mask to objectively identify the pattern of predicted oscillatory responses based on the active training data. This mask was then used to parse the EEG data obtained during pre and post passive listening conditions. Results indicate that mu suppression was significantly pronounced only in response to the trained melody sequence after motor learning, and that no significant suppression effects were observed within the other frequency bands (beta and gamma). Therefore, our findings support the idea that mu suppression can be observed and measured at the single-note level in non-musicians, and that this effect is frequency-band specific. Overall, these findings align well with the current literature on the proactive role of covert, predictive motor processing of time-sensitive regularities in support of auditory perception.

Our behavioural results demonstrate that subjects successfully learned the target melody and that this learning was sequence-specific (Figure 2). Supporting our principal hypothesis, we obtained significant mu suppression only during passive listening to the target melody post- compared to pre-training (Figure 4B). Moreover, this significant suppression was not found in the other two frequency bands, beta and gamma (Table 1). This greater post-training mu suppression while listening to the trained melody aligns with neuroimaging studies showing that passive listening to learned melodies elicits activity in motor areas (Baumann et al., 2007; Lahav et al., 2007; Lappe et al., 2008; Herholz et al., 2016). For example, Haueisen and Knösche (2001), demonstrated that passive listening to well-trained melodies increased activity over the contralateral M1 hand area, the putative generator of mu suppression (Pineda, 2013).

Our evidence for mu suppression in non-musicians after a single session of training additionally suggests that similar predictive models are developed over both short and long-term practice, and that these mechanisms are common to both musicians and non-musicians. This conclusion is supported by early spectral analyses showing that mu suppression emerges in most adults (Pfurtscheller & Aranibar, 1979), as well as functional connectivity studies indicating that the auditory and motor systems exhibit a strong resting functional connection in the brain that is independent of musicianship (Bedford et al., 2025).

The anticipatory nature of our mu suppression effect likely stems from the fact that it reflects *sequence-specific* activity (Kornysheva & Diedrichsen, 2014; Schubotz & von Cramon, 2002). Performing a musical piece involves manipulating a number of movements into an integrated motor sequence wherein events must be ordered correctly (Novembre & Keller, 2014), a process known as *sequencing* in motor control literature (Rosenbaum, 1991). At the cognitive level, this specific ability of the human brain to variably combine discrete units into rule-based, hierarchical sequences is sometimes described as *syntactic processing* (Bianco et al., 2016a), and there is reason to believe that it may be domain-general (Koelsch, 2011; Patel, 2003). Further, because elements in the sequence follow one another in specific orders, learning the inherent structure enables the prediction of upcoming sounds on the basis of current and previous sounds during perception (Mathias et al., 2015; Tillmann, 2012), which in turn triggers an internal representation of the associated motoric sequence (Rizzolatti & Sinigaglia, 2010).

Importantly, for a sequence of motor predictions to be paired to a sequence of auditory predictions, specific auditory-motor associations must necessarily have been formed. Note that this is not a prerequisite condition during beat production and perception tasks (Iversen & Patel, 2008), where beta-mediated motor predictions arise during natural production and listening (Fujioka et al., 2015), as well as when meter representations are manipulated internally even in the absence of movement (Morillon & Baillet, 2017). For this reason, we argue that the mu suppression observed in our study specifically reflects the prior establishment of auditory-motor associations, and that this is why it is seldom observed alongside beta activity in beat-perception tasks. By the same token, our findings support the notion that predicting *which* event will occur next within a sequence places different demands on cortical motor areas than simply predicting *when* a given event will occur based solely on periodicity (Novembre & Keller, 2014; Stupacher et al., 2013).

Our pattern of results aligns particularly well with the mu suppression reported in musicians (Wu et al., 2016), yet contrasts with the null effect reported in non-musicians by the same authors (Wu et al., 2017). Three methodological differences may account for this discrepancy. First, Wu et al. (2017) did not use active mu suppression data to localize suppression during passive listening. Our results suggest that leveraging the active larger mu suppression may be necessary for isolating the potentially fainter passive mu suppression in non-musicians. Second, given a sample size of only 13 subjects, the authors may have lacked statistical power to detect the comparably subtler passive mu suppression. Finally, training and passive exposure occurred in separate sessions in Wu et al. (2017), suggesting that suppression in non-musicians may be short-lived or more easily detected immediately after training, as done in the current study.

In the current study we did not observe correlations between mu suppression and changes in accuracy or RT. If mu suppression is an index of motor prediction or preparation, we would expect greater gains in performance to be related to greater post-training suppression. Thus, it is possible that performance might be more closely linked to individual differences in peaks or latencies in mu that were not captured by our group-level time-frequency mask.

One key strength of our study is that we created a time-frequency mask to identify active mu suppression in the motor training task, allowing us to constrain the time-frequency-channel space to reveal mu suppression during passive listening. The pattern of time-frequency modulations observed in the active condition is consistent with the frequency range typically ascribed to the mu rhythm (9-16.5 Hz; Pfurtscheller & Lopes da Silva, 1999). Although the mu rhythm is often defined within the 9-13 Hz range, several studies extend this range up to ~16 Hz (Wilson et al., 2010; Woodruff et al., 2011), and reviews likewise report broader definitions such as 10-14 Hz (Hobson & Bishop, 2017). Furthermore, the mu activity observed in our data is clearly distinct from lower beta activity, as the two bands are separated by several frequency bins across most channels (Fig. 3B). Similarly, the spatial extent of our mu partition is globally consistent with the theoretical mu suppression topography, given that we obtained a clustering of left-central channels around M1—the putative generator of mu rhythms (Pfurtscheller & Neuper, 1997), as supported by evidence from intracranial EEG recordings (Jasper & Penfield, 1949), MEG source-space analysis (Salmelin & Hari, 1994), and cortex-muscle coherence (Salenius et al., 1997). This being said, it is important to note that sensor-level EEG has a limited capacity to pinpoint exact neural sources and generators, especially when compared to source-resolved MEG (Baillet, 2017).

At first glance, our chosen timeframe of -650 to -100 milliseconds with respect to tone onsets may seem misaligned with the longer onsets of -2000 milliseconds typically reported in classical mu suppression studies (Pineda, 2005). However, given the short inter-onset interval in our task (1500 milliseconds) and the note-by-note scale of analysis, we note that to our knowledge no clear benchmark for finger-level mu suppression exists (Fox et al., 2016). Nonetheless, our time window appears appropriate as it is highly consistent with other metrics of motor preparation. For instance, the onset of mu activity in our motor task (Figure 3B) closely overlaps with the onset of around -400 milliseconds of the late component of the lateralized readiness potential (LRP), an ERP marker of motor preparation that also originates in M1 and lateralizes contralaterally to the effector (Shibasaki & Hallett, 2006; Trevena & Miller, 2002).

Importantly, the temporal mid-point of the observed mu-band suppression also coincides with the timing of the motor-evoked potentials (MEPs) elicited during post-training passive listening in our previous study using the same paradigm (Stephan et al., 2018). MEPs index motor excitability in M1 and have been used to measure the degree of motor preparation in the system in similar musical contexts (D’Ausilio et al., 2006). Moreover, the MEPs elicited in our previous study were effector-specific, just as the mu suppression observed in our current study is linked to the anticipation of specific notes, and therefore to specific effectors. Moreover, our findings align with prior MEG findings in passive listening to trained melodies, where distinct spatial responses were found for notes associated with the thumb versus pinkie fingers that matched the homuncular organization in M1 (Haueisen and Knösche, 2001). Thus, mu suppression may be linked to MEPs, as they both share a common generator in M1 and similar timing (cf. Lepage et al., 2008).

Besides M1, there are reasons to believe that the mu suppression we observed may be contingent on the co-activation of vPMC. On the one hand, because our task required the learning of a fixed, one-to-one sound-movement mapping; the kind of mapping that has been functionally tied to vPMC (Zatorre et al., 2007). Moreover, hand-related representations dominate vPMC's body map (cf. Graziano et al., 2002) and are thought to support fine motor skills (Rizzolatti et al., 2002), not directly through corticospinal projections but indirectly by modulating excitability in M1 (Davare et al., 2009, Buch et al., 2010). On the other hand, prior fMRI literature has established that vPMC is tied to goal-related action programming (Nieuwenhuys et al., 2008) specifically when instantiated via action sequencing (Rosenbaum, 1991), as required in our task. Indeed, inferior frontal gyrus and adjacent vPMC are thought to comprise a domain-general "grammar processor" involved in the structural sequencing of language (Pattel, 2003), music (Maess et al., 2001; Sammler et al., 2011), and action (Clerget et al., 2009; Fazio et al., 2009). However, BOLD activity in dPMC and nearby motor areas has been concurrently tied to mu suppression (Arnstein et al., 2011). Thus, while vPMC involvement appears most plausible, we cannot rule out a broader dorsal auditory-motor network contribution that may accompany or modulate the effect observed here.

Our finding that active mu suppression preceding movement shares time-frequency coordinates with mu suppression during passive listening to the same auditory stimuli is consistent with prior work demonstrating substantial neural overlap between action and perception (Keller & Koch, 2006), particularly within M1 (Fadiga et al., 2005; Arnstein et al., 2011; Pineda et al., 2013). Moreover, this overlap in our results reinforces two important lines of research. First, it strengthens the body of work linking mu suppression to motor imagery and mental simulation, a domain that has been comparatively less explored than mu suppression associated with overt self-movement and action by others (Pineda, 2005). Second, our finding lends mechanistic support to the *common coding* theory (Prinz, 1997), which proposes that perception and action rely on shared representational substrates. This is noteworthy because, while the notion of a unifying mechanism for perception and action has a rich history (James, 1890) and profound implications for human cognition (Hommel et al., 2001), the neural functioning and implementation of such a mechanism are not yet fully understood (Novembre & Keller, 2018).

Finally, while regularity-based *auditory* predictions during music listening have been thoroughly investigated (Rohrmeier & Koelsch, 2012; Tillmann, 2012), the neural basis of *motor* predictions in musical actions has not been explored in depth (Maidhof et al., 2009; Ruiz et al., 2009). Thus, our findings in non-musicians shed light on the neural dynamics of motor predictions during passive listening of learned melodies, indicating they are likely part of innate mechanisms that are globally important for perception (Patel & Iversen, 2014), and therefore dissociable from musical training.

## CONCLUSION

The present study provides evidence that mu suppression—an index of motor planning—increased during passive listening to a target melody post-training. Notably, changes in mu suppression were measured at the single-note level, showing that individual pitches in a trained melody predictively trigger a representation of the associated movements. Further, because we tested non-musicians, our results demonstrate that auditory-motor coupling and the related mu suppression is linked to both short- and long-term training. These findings support the concept of joint auditory-motor representations where sounds are linked to the actions required to make them.

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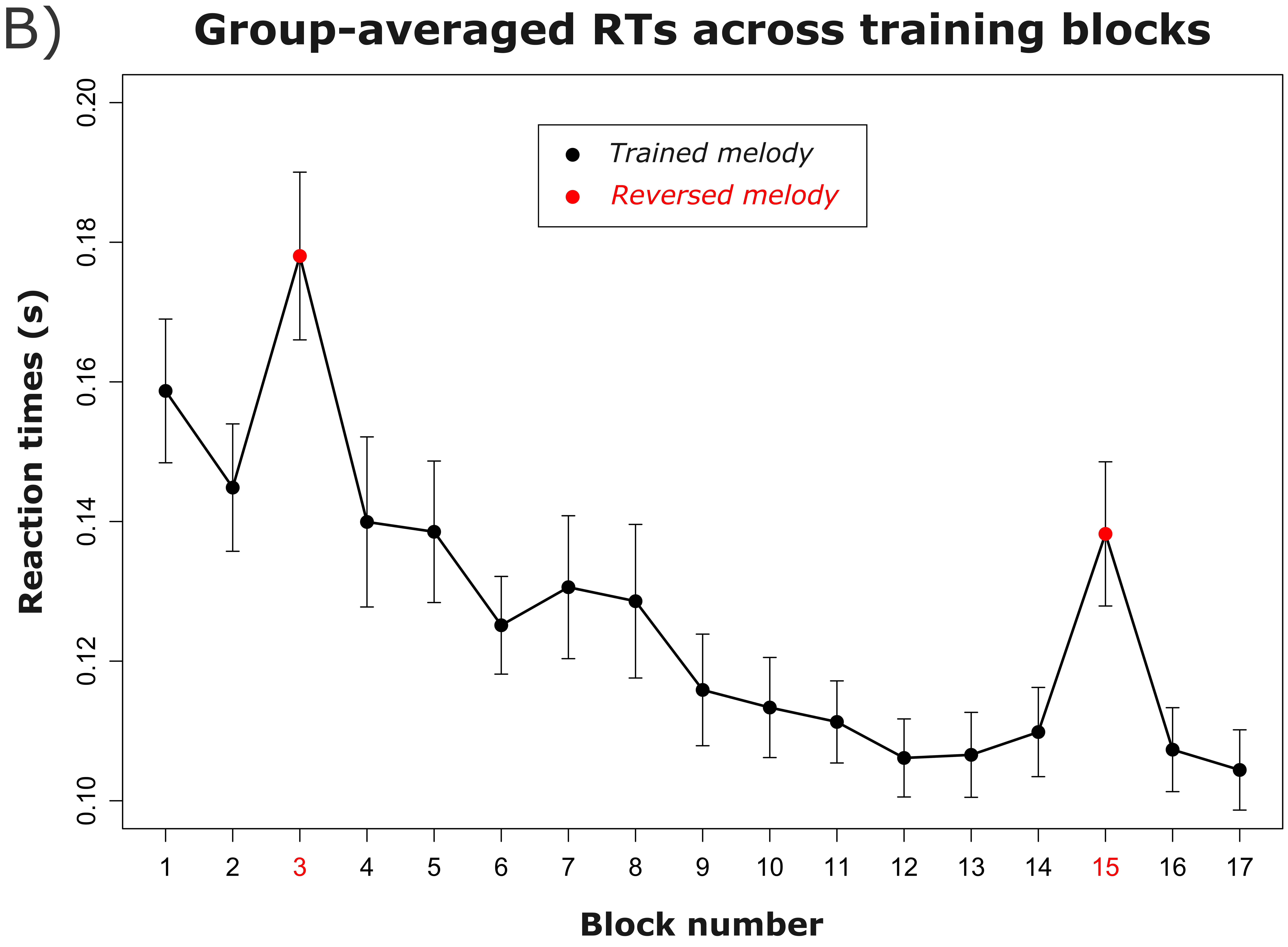
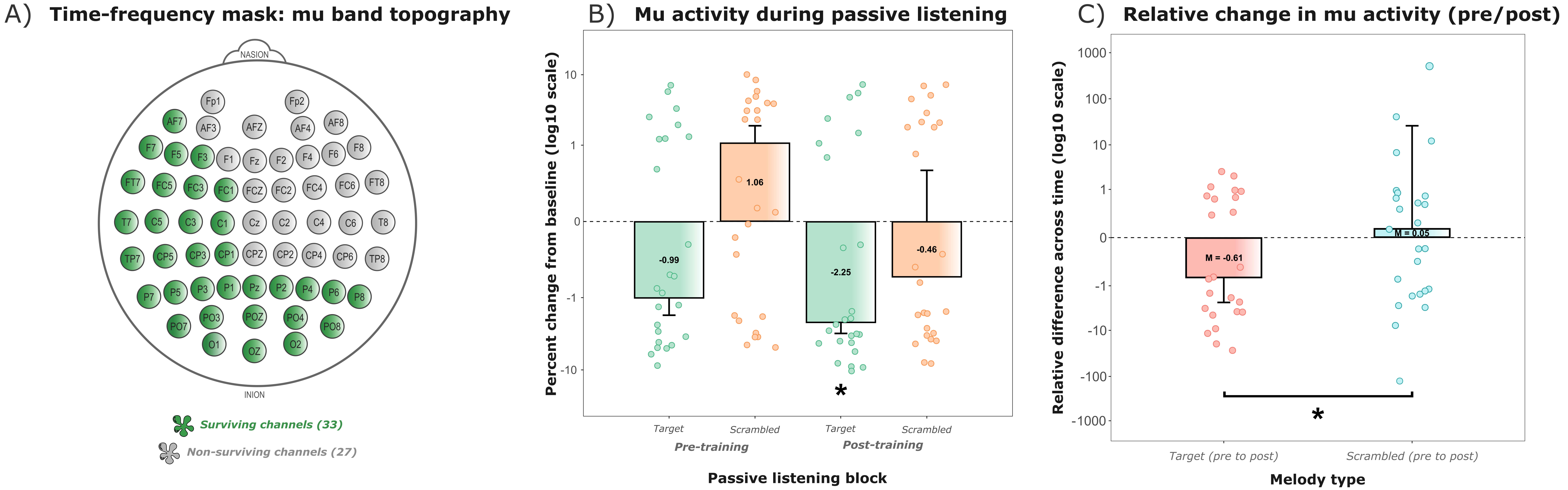
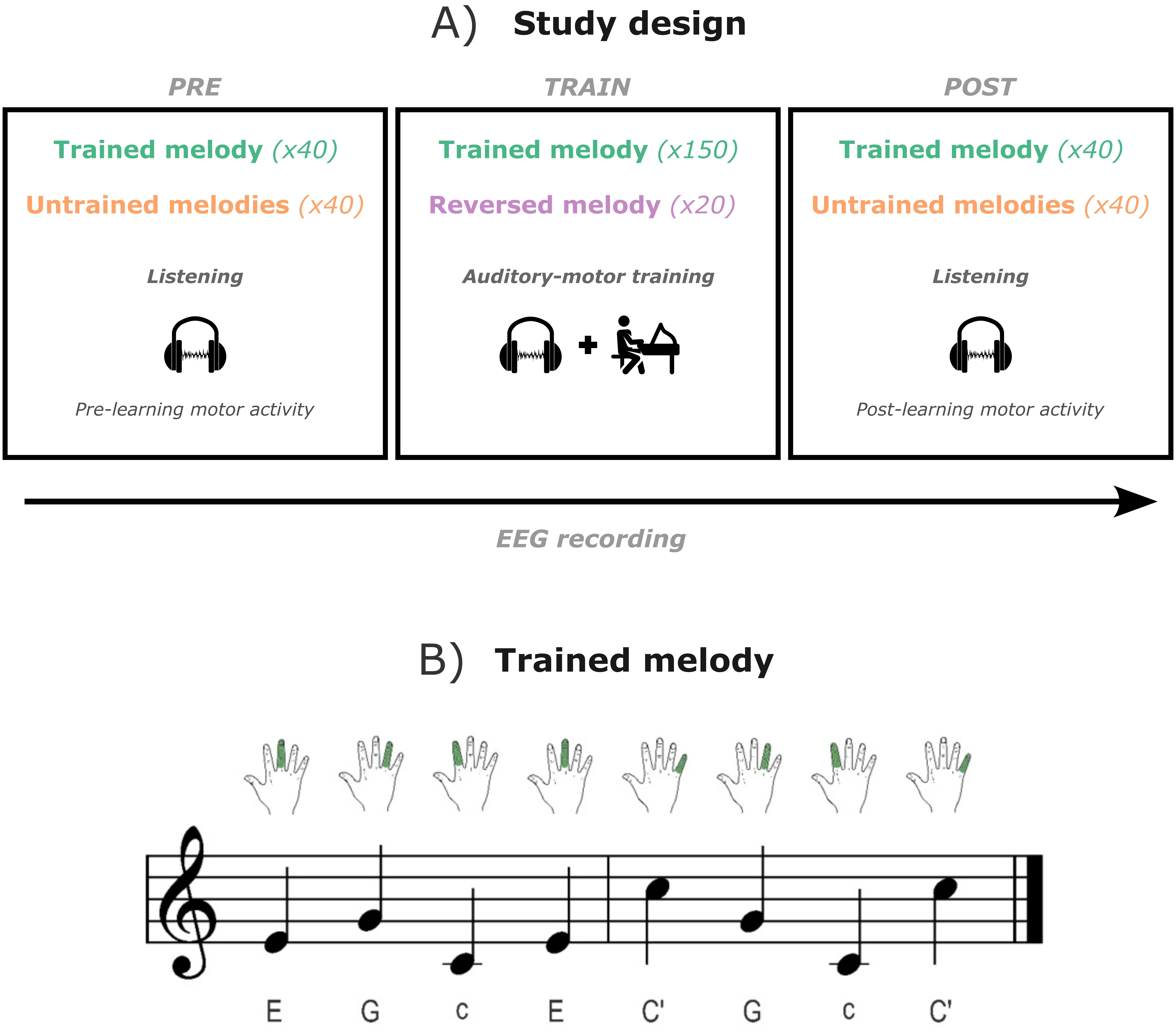
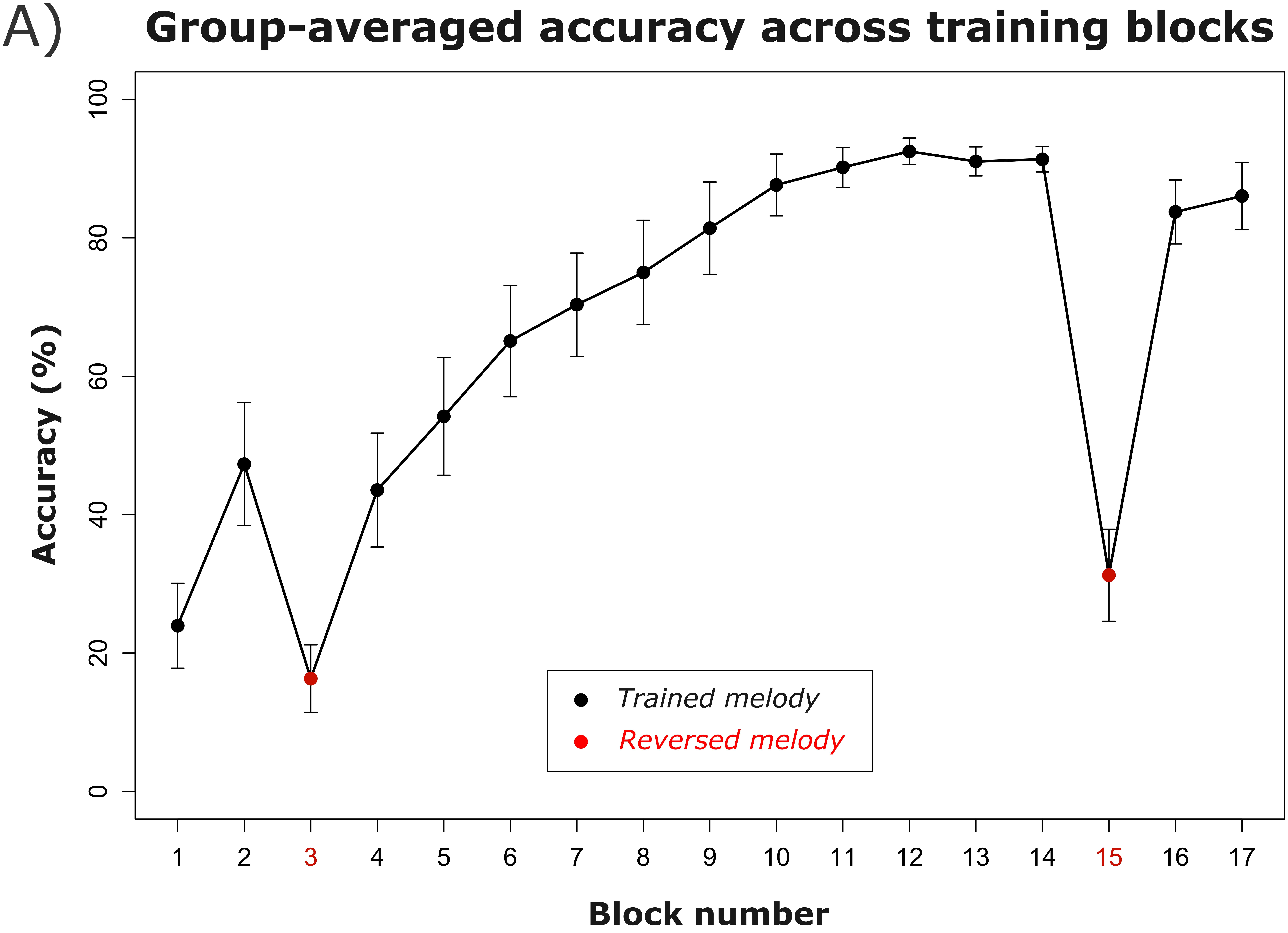

B)
Group-averaged RTs across training blocks
Trained melody
Reversed melody
Reaction times (s)
0.10
0.12
0.14
0.16
0.18
0.20
Block number
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17

A) Time-frequency mask: main cluster topography

B) Time-frequency activity in channel C3


A)
Time-frequency mask: mu band topography
NASION
Fp1
Fp2
AF7
AF3
AFZ
AF4
AF8
F7
F5
F3
F1
Fz
F2
F4
F6
F8
FT7
FC5
FC3
FC1
FCZ
FC2
FC4
FC6
FT8
T7
C5
C3
C1
Cz
C2
C4
C6
T8
TP7
CP5
CP3
CP1
CPZ
CP2
CP4
CP6
TP8
P7
P5
P3
P1
Pz
P2
P4
P6
P8
PO7
PO3
POZ
PO4
PO8
O1
OZ
O2
INION
Surviving channels (33)
Non-surviving channels (27)
B)
Mu activity during passive listening
Percent change from baseline (log10 scale)
10
1
0
-1
-10
-0.99
1.06
-2.25
-0.46
*
Target
Scrambled
Target
Scrambled
Pre-training
Post-training
Passive listening block
C)
Relative change in mu activity (pre/post)
Relative difference across time (log10 scale)
1000
100
10
1
0
-1
-10
-100
-1000
M = -0.61
M = 0.05
*
Target (pre to post)
Scrambled (pre to post)
Melody type


A) Study design
PRE
TRAIN
POST
Trained melody (x40)
Untrained melodies (x40)
Listening
Pre-learning motor activity
Trained melody (x150)
Reversed melody (x20)
Auditory-motor training
Trained melody (x40)
Untrained melodies (x40)
Listening
Post-learning motor activity
EEG recording
B) Trained melody
E
G
c
E
C'
G
c
C'


A)
Group-averaged accuracy across training blocks
Accuracy (%)
0
20
40
60
80
100
Block number
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
● Trained melody
● Reversed melody