Title:

Neural entrainment predicts the anticipatory P300 component during musical meter perception: An EEG study using dual-meter sound stimuli

Abbreviated title:

Neural entrainment predicts P300 during meter perception

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Number of pages: 26, **Number of figures:** 3, **Number of tables:** 3
Number of supplemental figures: 3, **Number of supplemental texts:** 1
Number of words: Abstract; 233, Introduction; 621, Discussion; 1336

Conflict of interest:

The authors have declared that no competing interests exist.

Acknowledgments:

This work was supported by grants from JSPS KAKENHI (grant numbers 23H05428 to KO, 23K18475 and 24H00735 to ROT, and 24KJ1930 to SK). The authors would like to thank Drs. Hironori Nakatani and Reiko Shiba for their valuable feedback on the early versions of our pilot experiment. We would also like to thank Dr. Shinya Fujii and the members of his laboratory for their insightful comments on the preliminary results of this study.

Abstract

Meter, the organization of beats into regular groupings, is a core element of music perception. Switches in meters frequently occur in music, reflecting the interplay between top-down attentional processes and the bottom-up processing of acoustic features. To disentangle this interplay in meter perception, we had previously invented a sound stimulus that simultaneously contained two meters. This dual-meter stimulus consisted of band-limited noise bursts that varied in center frequency and duration, with one feature following a triple-meter pattern and the other following a quadruple-meter pattern. Thus, the perceived meter switches between the two by changing attention from one acoustic feature to another, even when listening to identical stimuli. Using these stimuli, we here demonstrated the neural processes involved in meter perception by recording electroencephalogram (EEG) signals, while dissociating the influence of acoustic differences. We first found that the perceived meter structure was reflected in the entrained neural oscillations by comparing the spectral profiles of EEG signals when the participants focused on triple-meter versus quadruple-meter features. Second, an event-related potential component for anticipation (P300) was observed when the expected meter structure was disrupted by altering the frequency or duration of one sound at the end of the stimulus. Finally, individuals with stronger neural entrainment exhibited larger P300 responses to these disruptions. Our findings suggest that top-down attention modulates anticipation of the meter structure, and this anticipation induces neural entrainment that is involved in meter perception.

***Keywords**:*
meter, dual-meter stimuli, electroencephalogram, neural entrainment, P300

Significance Statement

Understanding how neural entrainment and anticipation interact is central to uncovering how the brain predicts and interprets incoming information. Musical meter provides an ideal model for investigating this process, as it emerges from the integration of bottom-up acoustic processing with top-down attention. However, traditional approaches have struggled to disentangle attention-driven neural entrainment and anticipation from acoustic variability. To address this, we introduced novel “dual-meter” stimuli that can be perceived as different meters depending on whether listeners attend to frequency or duration. EEG recordings revealed that neural entrainment to the perceived meter predicts the brain’s anticipatory P300 response to metrical violations, suggesting that attention links neural entrainment and anticipatory processing.

Introduction

Meter is one of the core elements of music perception that emerges from its ability to extract regular beats and assign varying levels of subjective intensity to them, thereby forming organized groupings (Cooper & Meyer, 1963; Fujii & Schlaug, 2013; Honing, 2013; Kotz et al., 2018; Large & Jones, 1999; Lerdahl & Jackendoff, 1983; London, 2012; Palmer & Krumhansl, 1990; Patel, 2006, 2010). In a duple meter found in march music, beats follow a recurring "strong(s)-weak(w)-s-w-…" pattern. The triple meter organizes beats as "s-w-w-s-w-w-…," which typically characterizes waltz music.

Meter perception involves both the bottom-up processing of acoustic features and top-down attentional mechanisms. A sound sequence such as "loud-soft-loud-soft…" is perceived as a duple meter, with louder sounds marking strong beats (Chen et al., 2006, 2009; Snyder & Large, 2005; Zatorre et al., 2007), elucidating the involvement of the bottom-up process. On the other hand, because music normally contains a variety of acoustic cues, actual meter perception should also require top-down selective attention to specific features. This is analogous to the "cocktail party effect" and auditory stream segregation, where listeners focus on a particular auditory stream among competing ones (Bregman, 1994; Bregman et al., 2001; Cherry, 1953). In our previous study (Kondoh et al., 2021), we tested this issue with "dual-meter" stimuli that allowed us to perceive two meters, which were created from sequences of band-limited noise bursts with varying center frequencies and durations. For instance, one of the stimuli had a frequency pattern "high-low-low…" to establish a triple meter while a duration pattern of "long-short-short-short…" corresponded to a quadruple meter at the same time. By instructing participants to shift their attention between frequency and duration, we found that listeners experienced different meters despite the physical sound sequences remaining intact. This result demonstrates that dual-meter stimuli offer a novel experimental paradigm for investigating the neural mechanisms of meter perception while dissociating the influence of acoustic variability.

Recent research suggests that neural entrainment and anticipatory processing are the key mechanisms underlying meter perception (Harding et al., 2025; Snyder et al., 2024; Vuust et al., 2022). Neural entrainment refers to the automatic synchronization of endogenous brain rhythms with external auditory inputs (Fujioka et al., 2009; Nozaradan et al., 2011), supporting bottom-up processing. At the same time, these oscillatory neural activities can shape the anticipation of future events according to dynamic attending theory (Ellis & Jones, 2009; Jones, 2018; Jones & Boltz, 1989). Thus, successful top-down selective attention to a particular feature of music may promote both neural synchronization

and anticipation specific to that feature, thereby forming a perception of the meter. Nonetheless, empirical evidence for this mechanism remains unclear because of methodological constraints in isolating neural activity related to entrainment and anticipation from acoustic influence.

To address this gap, this study employed dual-meter stimuli in an EEG experiment. First, we compared the spectral power when participants attended to either frequency or duration, allowing us to assess neural entrainment to the perceived meter while minimizing the confounding effects of acoustic differences. Second, we analyzed event-related potentials (ERPs) elicited by violations of metrical expectations introduced by altering the frequency or duration of a single noise burst. Such violations are known to evoke mismatch negativity (MMN), which reflects the automatic detection of prediction errors, and P300, which is associated with the conscious evaluation of unexpected events (Koelsch et al., 2019; Näätänen et al., 1978; Sutton et al., 1965; Vuust et al., 2009). By comparing ERP amplitudes across attentional conditions, we aimed to identify components linked to anticipatory processing, rather than acoustic changes. Finally, we examined whether neural entrainment indices predicted the MMN and P300 amplitudes. We hypothesized that stronger neural entrainment would be associated with larger ERP responses, indicating a functional relationship between entrainment and anticipation.

Materials and Methods

Participants

Thirty-four participants (17 females; 19.8 ± 1.6 years old) were recruited for this study from March 9 to October 1, 2022. All participants reported normal hearing and no history of hearing impairments. Before participating, they received instructions regarding the study and signed a written informed consent form. This study was approved by the Ethical Review Committee for Experimental Research on Human Subjects at the Graduate School of Arts and Sciences, the University of Tokyo, Japan (#663). The sample size was determined a priori using G*Power 3 (Faul et al., 2007) to ensure sufficient power (0.80) for detecting medium effect sizes ($\alpha = 0.05$). The analysis focused on pairwise comparisons of neural entrainment indices, specifically examining spectral differences across meter-related frequency bands (see ***Statistics*** below).

Stimuli

We designed dual-meter stimuli (**Fig. 1A, B**) consisting of 24 band-noise bursts. Each burst had one of two center frequencies: a high frequency of 1600 Hz or a low frequency of 1400 Hz, resulting in a

frequency difference of 200 Hz. We also varied the duration of the bursts and classified them as long (150 ms) or short (50 ms) sounds, creating a duration difference of 100 ms. These specific frequency and duration differences were selected based on our previous study (Kondoh et al., 2021), which demonstrated that listeners were most likely to switch attention between acoustic features under these parameters. The inter-onset intervals (IOIs) were fixed at 300 ms. The bandwidth of the noise bursts was 120% of the center frequency, with rise and decay times of 10 ms.

We created two types of stimuli based on regularity patterns in center frequency and duration: frequency-triple stimuli (**Fig. 1A**), and frequency-quadruple stimuli (**Fig. 1B**). Participants were randomly assigned to one of these two stimulus categories, with half listening to the frequency-triple stimuli and the other half listening to the frequency-quadruple stimuli. In the frequency-triple condition, the frequency pattern repeated every three sounds ("high–low–low" or "low–high–high"), while the duration pattern repeated every four sounds ("long–short–short–short" or "short–long–long–long"). In contrast, the frequency-quadruple category featured a frequency pattern that repeated every four sounds ("high–low–low–low" or "low–high–high–high"), paired with a duration pattern that repeated every three sounds ("long–short–short" or "short–long–long"). Consequently, each category contained four stimulus subtypes determined by which sounds served as strong beats: high and long, high and short, low and long, and low and short (see **Fig. S1** for all stimulus types).

Pre-training to familiarize with dual-meter stimuli

Participants were familiarized with dual-meter stimuli for focusing on center frequency and duration differences by attending a web-based pre-training session at their home. In this pre-training, they were instructed to listen to a dual-meter stimulus and count specific target sounds. The target sound was instructed by showing a word, "high," "low," "long," or "short," on the computer screen before starting the stimulus presentation. The task of participants was to detect the instructed sound in the stimulus and count them. Each stimulus contained 3 to 32 sounds per trial, and included one to eight target sounds. After listening, participants reported the target count by selecting numbers from 1 to 8 on the screen.

The training consisted of six blocks of 32 trials (4 characteristics × 8 targets). In the high/low counting trials, the frequency difference remained at 200 Hz, whereas the duration difference increased from 64 ms in the first and second blocks to 80 ms in the third and fourth blocks, rendering the frequency difference less prominent. Conversely, in the long/short counting trials, the duration difference

remained at 100 ms, whereas the frequency difference increased from 128 Hz in the first and second blocks to 160 Hz in the third and fourth blocks, making the duration difference less pronounced. In the final two blocks, both tasks used stimuli with a frequency difference of 200 Hz and a duration difference of 100 ms, matching the parameters used in the EEG recording. No feedback on the correct answers was provided during the training. The training program was developed using lab.js (Henninger et al., 2022), and the participants completed the program individually on their personal computers using headphones. To verify the use of headphones, we used a pre-set screening test (Woods et al., 2017).

EEG recording

During the EEG recording session, the participants were asked to listen to the dual-meter stimuli while attending to differences in either frequency or duration without any explicit response (**Fig. 1C**). To violate metrical anticipation, the center frequency or duration of the 19th, 20th, or 21st band-noise bursts was modified ('altered' in **Fig. 1C**; see **Fig. S2** for all alterations). For comparison, 'standard' sounds were defined as those with both center frequency and duration matching the altered sounds. We further discriminated the following two situations: one was the 'violated' condition, where changes in the attended acoustic feature disrupted metrical anticipation, and the other was the 'unviolated' condition, where the metrical structure remained intact despite modifications.

Each trial began with 0.8 seconds of silence followed by a 7.2-second stimulus presentation. A block consisted of 14 trials that focused on one acoustic feature, including six trials for each of the violated and unviolated conditions, and two trials for stimuli with no alteration. Throughout each block, a fixation cross and a display indicating the target feature were shown on the screen. Each session comprised four blocks with randomized stimulus assignments and trial orders, and the participants completed a total of four sessions.

EEG recordings were performed using a 32-channel EasyCap and BrainAmp DC system (Brain Products GmbH, Germany) with a sampling rate of 1000 Hz. The electrodes were positioned at C3, C4, CP1, CP2, CP5, CP6, Cz, F3, F4, F7, F8, FC1, FC2, FC5, FC6, FT10, Fp1, Fp2, Fz, Iz, O1, O2, P3, P4, P7, P8, PO10, PO9, Pz, T7, and T8. In addition, an electrode (AFp10) was placed near the right eye to record the electrooculogram activity, and reference electrodes were attached to the left (A1) and right (A2) earlobes. Stimulus presentation was controlled using Presentation 18.1 software (Neurobehavioral Systems, Inc., USA). Instructions about the attended acoustic feature and the

fixation cross were presented on a 24-inch LCD monitor (XL2420T, BenQ, Taiwan), with participants seated approximately 80 cm from the screen. Auditory stimuli were delivered binaurally through earphones (Compumedics Neuroscan Inc., USA) at approximately 70 dB SPL via an external sound card (UA-22, Roland, Japan).

Analysis

Preprocessing on EEG signal

Preprocessing was performed using MATLAB R2023b and EEGLAB v2022.1 (Delorme & Makeig, 2004). EEG data obtained from electrodes with impedance values greater than 15 kΩ were excluded from analysis. The raw signal was filtered with a high-pass filter set at 0.5 Hz and a low-pass filter set at 30 Hz. The independent component analysis (ICA) was then performed to decompose the EEG data into a number of components equal to the number of electrodes (Delorme et al., 2007; Makeig et al., 2004). The ICLabel tool was used to classify these components as either brain-derived signals or noise sources, including ocular, muscular, and cardiac activities, as well as line noise (Pion-Tonachini et al., 2019). For subsequent analyses, only the components exhibiting more than 50% brain-derived signals were retained.

Neural entrainment to meter

The neural entrainment to meter patterns was assessed by the following three steps: obtaining spectra, selecting appropriate electrodes, and calculating meter-related components. EEG data corresponding to the first 18 noise bursts of the dual-meter stimuli (total 5.4 s) in each trial were used for assessing neural entrainment. A moving median filter with a 1.2-second window was applied to detect and eliminate slow drifts. The beginning and last parts of the EEG signal were then tapered using a raised cosine (rise time: 0.9 s; decay time: 0.3 s) to reduce side-lobe effects in the spectra. The data were downsampled to a sampling rate of 40 Hz for computational efficiency. Then, a Fast Fourier Transform (FFT) was performed at 1,728 points (with 8-time interpolation) to obtain amplitude spectra with a frequency resolution at 0.023 Hz (40 Hz / 1,728 points).

We then selected appropriate electrodes by identifying neural oscillations with a frequency of the stimulus IOI (300 ms). We compared the grand means of EEG spectra with the surrogate baseline spectrum for each electrode. This surrogate signal was generated by randomly shuffling the original EEG data for every 300-ms time slots, and underwent the same tapering and FFT processes (**Fig. 2A**). For each electrode, we computed an amplitude ratio of the spectral component at 3.33 Hz (ranging

from 2.83 to 3.83 Hz) in the original signal to that in the surrogate signal. We selected an electrode with the highest ratio and surrounding electrodes and averaged their signals for further neural entrainment analysis (**Fig. 2B**).

After selecting electrodes, we calculated an index reflecting the meter-related neural entrainment. We defined five frequency bands (Band-1 to Band-5), centered at 3.33 Hz (range 3.26–3.43 Hz), 1.67 Hz (1.60–1.76 Hz), 1.11 Hz (1.04–1.20 Hz), 0.83 Hz (0.76–0.93 Hz), and 0.67 Hz (0.60–0.76 Hz), respectively (**Fig. 2C**). Band-1, 3, and 4 corresponded to the regularities of the beat, triple meter, and quadruple meter, respectively. We computed the amplitude of each band in the mean EEG signal from selected electrodes when participants attended to triple-related features or quadruple-related features, and then, calculated the difference between them (**Fig. 2D**). The amplitude difference is more positive when there is stronger neural entrainment to the triple feature. It is more negative when there is stronger entrainment to the quadruple feature.

Event-related potentials

For the analysis of event-related potentials associated with metrical anticipation, we selected appropriate electrodes by identifying strong neural responses to the altered sound in stimulus sequence. We computed the average signals for each of standard and altered sounds irrespective of the difference between violated and unviolated conditions (**Fig. 3A**), applying the analysis window of 0–600 ms after the sound onset with the baseline correction using the mean amplitude between 100 and 0 ms prior to sound onset. The electrode exhibiting the largest difference between the standard and altered sounds, along with its neighboring electrodes, was chosen for further ERP analysis (**Fig. 3B**). We employed this selection criterion to ensure that the EEG data contained the neural response that reflected the bottom-up process for detecting acoustic differences.

ERPs were then obtained by averaging the signals for both the altered and standard sounds under each condition. We subtracted the ERP elicited by standard sounds from that elicited by altered sounds to assess whether the MMN and P300 components reflected violations of the anticipatory metrical structure induced by the altered sounds, while controlling for acoustic variability. We defined the time windows at 190-350 ms and 351-600 ms after the sound onset to assess MMN and P300, respectively (shown as bold black bars in **Fig. 3F**).

Statistics

For assessing the neural entrainment to meter patterns, we tested whether the amplitude differences between situations in which participants attended to triple- versus quadruple-related acoustic features were not constant across frequency bands. The data were fitted using a linear mixed-effects regression model, with spectral difference as the dependent variable, meter-related frequency band as a fixed effect, and participant ID as a random effect. We used the 'lmer' function in the 'lme4' package (ver. 1.1.35.1) (Bates et al., 2015), with significance tests were conducted by 'lmerTest' package (ver. 3.1.3) (Kuznetsova et al., 2017). After fitting the model to the data, we conducted pairwise comparisons between meter-related frequency bands using the 'emmeans' package (ver. 1.10.3) (Lenth, 2024). *P*-values of multiple comparisons were adjusted by Tukey-Kramer method (denoted as p_{Tukey}).

For the analysis of ERPs reflecting violation of metrical anticipation, we tested whether the amplitude difference (altered versus standard sounds) in the violated condition was not the same as that in the unviolated condition. The average amplitude differences of the two conditions were compared using a paired t-test after confirming a normal distribution; a paired Wilcoxon test was used if normality could not be confirmed.

To explore the relationship between neural entrainment and anticipatory processes, we assessed correlations of their indices. For neural entrainment, we focused on Bands 3 and 4, computing a band-specific spectral difference by subtracting the spectral difference in Band 4 from that in Band 3. A positive value indicates that neural activity is more strongly entrained to the triple-related feature in Band 3, whereas a negative value indicates stronger entrainment to the quadruple-related feature in the same band. We predicted that this band-specific spectral difference would reflect meter-related neural entrainment the most. For anticipatory processing, we calculated the amplitude difference between the original amplitude differences in the violated and unviolated conditions, and averaged separately for the MMN and P300 time windows. Two linear models were constructed: one with the MMN amplitude difference as the response variable, and the other with the P300 amplitude difference as the response variable, using the band-specific spectral difference as the explanatory variable. All statistical tests were two-sided and performed using the R software (R Core Team, 2024) (version 4.1.1), with the significance level set at $\alpha = 0.05$.

Results

The present study aimed to elucidate the neural mechanisms underlying meter perception using dual-meter stimuli (**Fig. 1A,B**), which consisted of band-limited noise bursts varying in center frequency and duration. This design allows the same physical sound sequence to elicit different metrical interpretations, depending on whether listeners attend to frequency or duration differences (**Fig. 1C**), thereby dissociating the effects of acoustic variability from neural processing. We compared the spectral profiles of EEG signals when participants focused on triple-meter versus quadruple-meter features to assess the neural oscillations associated with the metrical structure. We then calculated ERPs in response to disruptions of the anticipated metrical structure, implemented by altering the frequency or duration of one sound later in the stimulus. We also examined whether neural entrainment predicted the responses to metrical violations.

Neural entrainment related to meter

To examine the neural entrainment related to the meter, we first selected electrodes for analysis. We computed the EEG spectrum using data from the initial 18 noise bursts, irrespective of whether participants attended to the center frequency or duration differences (**Fig. 2A**). We generated a surrogate signal and calculated its spectrum as a comparison. We then focused on the frequency of approximately 3.33 Hz (ranging from 2.83 to 3.83 Hz), which reflects neural entrainment to each noise burst (beat), and compared the ratio of the original to surrogate signals. The highest ratio, averaged across participants, was observed at electrode T7 (-0.02 ± 0.01; mean ± SD) (**Fig. 2B**). Based on these findings, T7 and its neighboring electrodes, FC5 (-0.03 ± 0.01), C3 (-0.03 ± 0.02), and CP5 (-0.03 ± 0.02), were selected for further analysis.

Within the same time window, we computed the EEG spectral amplitude while categorizing the data according to whether the participants attended triple- or quadruple-related acoustic features. We averaged the spectral amplitudes from T7, FC5, C3, and CP5 and defined five frequency bands corresponding to meters (**Fig. 2C**): Band-1 (beat frequency) at 3.33 Hz (ranged 3.26–3.43 Hz); Band-2 at 1.67 Hz (1.60–1.76 Hz); Band-3 (triple) at 1.11 Hz (1.04–1.20 Hz); Band-4 (quadruple) at 0.83 Hz (0.76–0.93 Hz); and Band-5 at 0.67 Hz (0.60–0.76 Hz). To assess whether the participants' EEG signals were entrained to the triple- or quadruple-related acoustic features of the dual-meter stimuli, we calculated the amplitude difference by subtracting the amplitude associated with attention to quadruple features from that associated with attention to triple features (**Fig. 2D**). The overall

amplitude difference values (mean ± SD) of Band-1 to Band-5 were $-1.14 \times 10^{-3} \pm 3.25 \times 10^{-3}$ μV, $0.14 \times 10^{-3} \pm 3.16 \times 10^{-3}$ μV, $2.30 \times 10^{-3} \pm 5.41 \times 10^{-3}$ μV, $0.39 \times 10^{-3} \pm 4.59 \times 10^{-3}$ μV, and $-0.19 \times 10^{-3} \pm 3.76 \times 10^{-3}$ μV, respectively (**Fig. 2E**). To determine whether the amplitude differences varied across the frequency bands, we fitted the data to a linear mixed-effects regression model with spectral difference as the objective variable, the meter-related frequency band as a fixed effect, and participant ID as a random effect. The model revealed a significant effect of the spectral bands ($F(4, 132) = 3.52$, $p = 0.009$). Band 1 showed significantly lower spectral difference values compared to Band 3 (*estimate* $= -3.44 \times 10^{-3}$, $SE = 0.95 \times 10^{-3}$, $t(132) = -3.62$, $p_{Tukey} = 0.004$, **Table 1**). Other pairwise comparisons were not significant ($p_{Tukey} > 0.05$), although the contrast between Bands 3 and 5 approached significance ($p_{Tukey} = 0.073$). These results suggest that the overall amplitude difference reflects neural entrainment to the acoustic features that form meter perception.

Event-related potentials

To measure the extent of the participants' metrical anticipation, we modified the center frequency or duration of the 19th, 20th, or 21st band-noise bursts, referred to as altered sounds, and defined standard sounds as those in which both the center frequency and duration matched the altered sounds (**Fig. 1C**). Thus, when participants focused on the altered acoustic feature, the metrical structure was violated (violated condition). In contrast, when the participants focused on the other feature (unviolated condition), the metrical structure remained intact despite the modifications.

To identify the electrodes for analyzing the neural processes associated with meter anticipation, we first calculated the ERPs for standard and altered sounds (**Fig. 3A**), and computed the amplitude difference (altered minus standard) for each electrode (**Fig. 3B**). The largest difference was observed at electrode Fz (−0.90 ± 0.46 μV; mean ± SD). Consequently, Fz and its neighboring electrodes, F3 (−0.76 ± 0.36 μV), F4 (−0.90 ± 0.38 μV), FC1 (−0.75 ± 0.45 μV), FC2 (−0.89 ± 0.46 μV), and Cz (−0.75 ± 0.43 μV), were chosen for further analysis.

Subsequently, we investigated the neural processes underlying anticipatory mechanisms in meter perception by calculating the ERPs for standard and altered sounds under both violated and unviolated conditions (**Fig. 3C,D**). For each condition, we computed the amplitude difference (altered minus standard) (**Fig. 3E**). For the MMN, the amplitude difference was −1.02 ± 1.51 μV in the unviolated condition and −0.65 ± 1.37 μV in the violated condition. For the P300, the potential difference was −1.03 ± 1.34 μV in the unviolated condition and −0.75 ± 1.39 μV in the violated condition. Although

the P300 component appeared larger in the violated condition, no statistically significant differences were found for either MMN ($V = 351$, $p = 0.370$) or P300 ($t = 0.90$, $df = 33$, $p = 0.374$).

Predicting the anticipatory process from neural entrainment

We examined whether neural entrainment predicts anticipatory mechanisms during meter perception by focusing on the band-specific spectral difference (Band 3 minus Band 4), which we considered to best reflect neural entrainment related to meter (**Fig. 2F**). For visualization purposes, we categorized the participants into three groups based on their band-specific spectral differences in descending order: good ($n = 11$), middle ($n = 12$), and poor switchers ($n = 11$). For each group, we calculated the amplitude difference by subtracting the amplitude difference in the unviolated condition from that in the violated condition. In the MMN time window, no prominent differences were observed between groups (**Fig. 3F**). In contrast, in the P300 time window, the good switchers exhibited larger amplitudes, followed by the middle and poor switchers (**Fig. 3F**). Linear regression models revealed that the band-specific spectral difference did not significantly predict the difference in the MMN amplitude (*slope* = 31.28, $p = 0.445$; **Fig. 3G**, **Table 2**), whereas it significantly predicted the difference in P300 amplitude (*slope* = 105.04, $p = 0.013$; **Fig. 3H**, **Table 3**). These findings suggest that attention shapes anticipation of metrical structures, enhances neural entrainment, and hence facilitates meter perception.

Discussion

This study aimed to clarify the neural mechanisms underlying meter perception using dual-meter sound stimuli, which were designed to dissociate acoustic influences from neural responses (**Fig. 1A,B**). First, we examined oscillatory neural entrainment by comparing EEG spectral profiles when participants selectively attended to either the triple- or quadruple-related features of the stimuli (**Fig. 2D**). We found that the overall amplitude differences varied significantly across meter-related frequency bands, suggesting the meter-related neural entrainment (**Fig. 2E**). However, the specific spectral difference between the frequency bands corresponding to the triple and quadruple meters, which was our primary interest, was not statistically significant (**Fig. 2E,F**). We also analyzed the MMN and P300 components of ERPs elicited by deviations in metrical structure. Although differences in ERP amplitudes were observed between conditions in which metrical expectations were violated and those in which they were not (**Fig. 3E**), these differences were not statistically significant. We then investigated whether the degree of neural entrainment predicted the magnitude of the anticipatory responses. Our results showed that the entrainment index significantly predicted the P300 amplitude but not the MMN

amplitude (**Fig. 3F–H**). These findings suggest that directing attention to specific acoustic features enhances the anticipation of metrical structures, which in turn engages the neural entrainment mechanisms involved in meter perception. Previous studies have proposed that neural entrainment and anticipatory processing are two core mechanisms supporting meter perception (Harding et al., 2025; Snyder et al., 2024; Vuust et al., 2022) and that entrainment may serve as a basis for anticipation, as described by the dynamic attending theory (Ellis & Jones, 2009; Jones, 2018; Jones & Boltz, 1989). Our study advances this framework by directly demonstrating a functional relationship between neural entrainment and anticipatory processing, which was made possible by the combined use of dual-meter stimuli and EEG measurements.

The lack of significant effects in the statistical tests for the band-specific amplitude differences (**Fig. 2F**), and for the amplitude differences between the conditions (**Fig. 3E**), which are indicative of the anticipatory process, is likely due to individual variability in top-down attentional processes. In our previous study (Kondoh et al., 2021), we observed individual differences in participants' ability to switch their attention between the frequency and duration of dual-meter stimuli. Those who had prior training to tap along each noise burst while focusing on a single acoustic feature exhibited greater switching ability. In the present study, the participants received pre-training to familiarize themselves with the stimuli, while the main task required them to count the number of sounds associated with a specific acoustic feature. Unlike in the previous study, the participants were not explicitly instructed to attend to frequency or duration contrasts, which may have allowed individual differences in attention control to influence the results. Moreover, the use of a broader range of stimuli compared to our previous study may have made it challenging for some listeners to shift their attention between acoustic features. Additionally, musical experience may affect the top-down processing of meter perception (Drake et al., 2000; Geiser et al., 2009; Kondoh et al., 2021). Because musical experience was not the primary focus of this study, we did not assess it using measures such as the Goldsmiths Musical Sophistication Index (Müllensiefen et al., 2014; Sadakata et al., 2022). Future research should investigate these factors to better explain the individual differences observed in the neural entrainment and anticipatory responses.

The band-specific amplitude differences reflecting neural entrainment did not predict amplitude differences between violated and unviolated conditions in the MMN time window (**Fig. 3G**); however, they significantly predicted the amplitude differences in the P300 time window (**Fig. 3H**). This

dissociation likely reflects the functional distinctions between the MMN and P300 components. MMN is typically associated with relatively pre-attentive detection of deviations in acoustic features (Koelsch et al., 2019; Näätänen et al., 1978, 2007; Vuust et al., 2022). Previous studies investigating bottom-up processing in meter perception have shown that disruptions to amplitude regularity in sequences establishing a duple meter, for example, inserting a pattern such as "loud-soft-loud-soft-loud-loud-soft…", can elicit MMN responses (Radchenko et al., 2023; Zhao et al., 2017). In the present study, the MMN may have primarily reflected the immediate acoustic change of a single manipulated noise burst rather than a violation of higher-order metrical expectations. In contrast, the P300 component reflects conscious evaluation processes following the detection of anticipation violations (Koelsch et al., 2019; Polich, 2007). Supporting this interpretation, prior studies have shown that violations of rhythmic expectations evoke stronger P300 responses in jazz musicians than in non-musicians, suggesting that the P300 is shaped by higher-order metrical evaluations and musical expertise (Vuust et al., 2009; Vuust & Witek, 2014). Thus, the P300 observed in this study likely reflects the violation of abstract metrical expectations rather than a response to simple acoustic deviance. This functional distinction may explain why neural entrainment predicts the P300 component but not the MMN.

Previous studies on neural entrainment related to meter perception have often relied on the amplitude of EEG signals at frequencies corresponding to the perceived meter, known as SSEPs (Chemin et al., 2014; Cirelli et al., 2016; Gibbings et al., 2023; Nave et al., 2022; Nozaradan et al., 2011, 2012, 2016, 2018). Typically, SSEP analysis involves applying FFT and calculating the amplitude at a target frequency by subtracting the average amplitude of its neighboring frequency bins. These neighboring bins served as a baseline for isolating frequency-specific activity. However, this method can limit the accuracy of comparisons across the frequency bins. In contrast, the present study introduced a novel approach by comparing the EEG spectra between conditions in which participants attended to either the center frequency or duration of the dual-meter stimuli. This approach enables direct comparisons across meter-related frequency bands while minimizing the confounding effects of acoustic variability. As a result, the overall amplitude differences reflected meter-related neural entrainment (**Fig. 2E**). Thus, in addition to traditional SSEP techniques, our method offers an alternative perspective that may enhance our understanding of attention-modulated neural entrainment in meter perception.

The present study had several limitations. First, this study used dual-meter stimuli with IOIs fixed at 300 ms (200 beats per minute or bpm) to maintain consistency with our previous study (Kondoh et al.,

2021). This setting is unlikely to be problematic for beat perception because earlier research has indicated an optimal tempo for beat perception ranging from 100 ms to 2 s in the IOI (London, 2012; Repp & Su, 2013). However, 200 bpm could be considered very fast in Western musical standards; thus, further research employing slower tempos is necessary to clarify its effects on neural entrainment and anticipatory responses during meter perception. Second, we did not rigorously assess the relationship between band-specific amplitude differences (reflecting neural entrainment related to meters), amplitude differences between conditions (reflecting expectancy violations), and the behavioral measures of meter perception. As an exploratory analysis, we examined the correlations between task sensitivity, measured by the ability to detect whether an altered sound disrupted metrical structures, and EEG indicators (**Text S1**, **Fig. S3**). However, because we did not have a priori hypotheses about specific electrode sites, we only reported electrodes with high correlation coefficients. Future studies should systematically test the relationship between EEG and behavioral indicators using the electrodes identified in our supplementary analysis.

In conclusion, this study investigated the neural basis of meter perception using dual-meter stimuli designed to minimize the confounding effects of acoustic variation on neural activity. We hypothesized that top-down selective attention to either the frequency or duration of a sound sequence modulates the bottom-up processing of that feature, leading to neural synchronization with acoustic regularities and the formation of corresponding expectations that support meter perception. Consistent with this hypothesis, we found that the strength of meter-related neural entrainment predicted the strength of anticipation. These findings represent a methodological advance in isolating neural responses to meters from acoustic confounds, and provide direct evidence linking neural synchronization to anticipatory processing in meter perception. We believe that these results mark an important step toward a deeper understanding of meter perception, which is a fundamental phenomenon in music.

Author Contributions

Conceptualization: SK, KO, ROT

Data Curation: SK

Formal Analysis: SK, ROT

Funding Acquisition: SK, KO, ROT

Investigation: SK

Methodology: SK, ROT

Project Administration: KO, ROT

Software: SK, ROT

Supervision: KO, ROT

Visualization: SK, ROT

Writing – Original Draft Preparation: SK

Writing – Review & Editing: SK, KO, ROT

Data Availability

The data supporting the findings of this study as well as the sound files of the dual-meter stimuli used are available from the Open Science Framework repository (https://osf.io/hw2y8).

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Figures

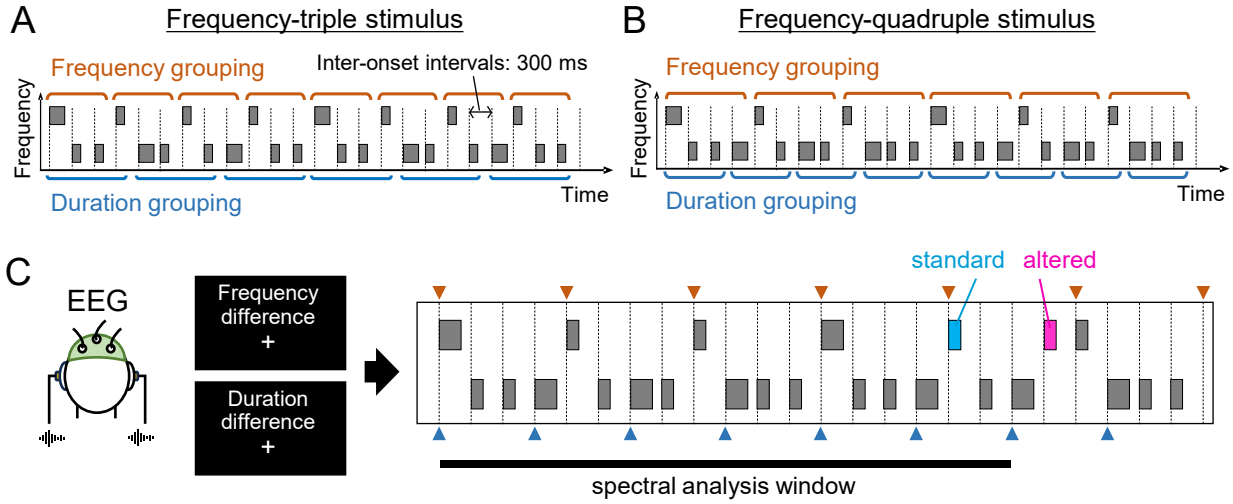

Fig 1. Schematic drawing of dual-meter stimuli and experimental design. A. Example stimulus from the frequency-triple category with "high-low-low-..." frequency and "long-short-short-short-…" duration patterns. **B.** Example stimulus from the frequency-quadruple category with "high-low-low-low..." frequency and "long-short-short-…" duration patterns. The center frequency of the higher sound was 1600 Hz and that of the lower sound was 1400 Hz, resulting in a frequency difference of 200 Hz. The duration of the longer sound was 150 ms, whereas that of the shorter sound was 50 ms, creating a duration difference of 100 ms. The bandwidth of each noise burst was 120% of its center frequency, and the inter-onset intervals (IOIs) were fixed at 300 ms. **C.** Experimental procedure. Participants attended to either the duration or frequency differences of the stimulus during electroencephalogram (EEG) recordings. Spectral analysis was performed on the EEG data corresponding to the initial 18 sounds (indicated by the black line). In this example, the 20th noise burst was altered by increasing its center frequency from low to high (altered sound is indicated by the pink square). We defined standard sounds as those that matched the altered sounds in center frequency and duration, presenting at least three sounds earlier (indicated by the light blue square). When focusing on the frequency difference, the metrical structure of the quadruple meter (indicated by orange triangles) is violated by the altered sound (violated condition). In contrast, when focusing on the duration difference, the metrical structure of the triple meter (indicated by blue triangles) remains intact (unviolated condition). Event-related potentials (ERPs) were calculated around the altered and standard sounds.

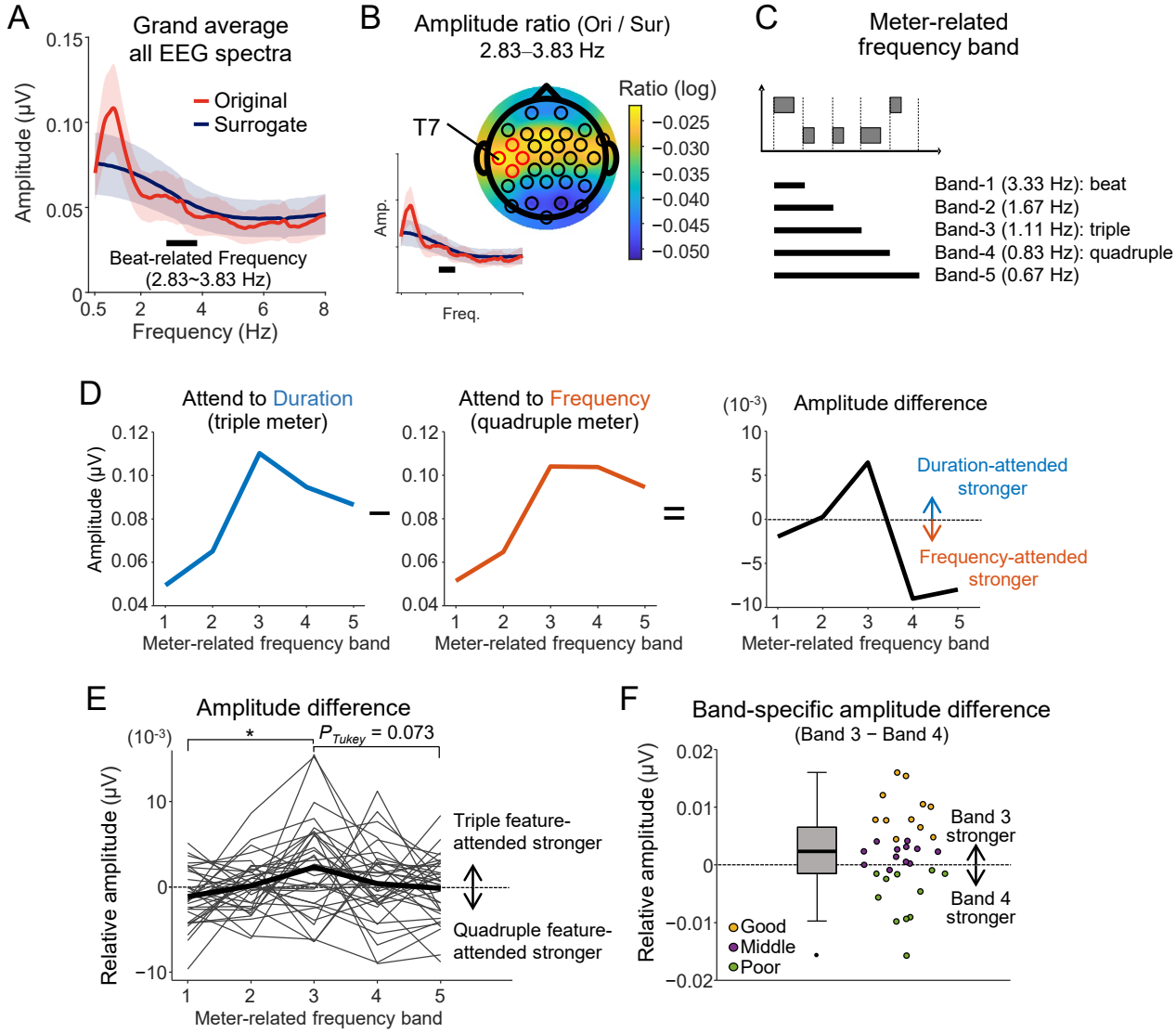

Fig. 2 Neural index reflecting entrainment associated with meter perception. A. Grand average of EEG spectra of the original and surrogate signals without differentiating whether participants focused on triple- or quadruple-related acoustic features. The shaded areas represent the standard deviations (SD) across the electrodes. The analysis targeted a beat-related frequency range (2.83–3.83 Hz). **B.** Topographical electrode distribution of the log-transformed ratio of the original to surrogate EEG signal amplitudes in the beat-related frequency range. The T7 electrode showed the highest ratio, and the adjacent electrodes, FC5, C3, and CP5, were selected for further analysis (indicated by red circles). **C.** Description of meter-related frequency bands: Band-1 (3.33 [3.26–3.43] Hz) corresponding to beat, Band-2 (1.67 [1.60–1.76] Hz), Band-3 (1.11 [1.04–1.20] Hz) corresponding to the triple meter, Band-4 (0.83 [0.76–0.93] Hz) corresponding to the quadruple meter, and Band-5 (0.67 [0.60–0.76] Hz). **D.** Spectral analysis to calculate neural entrainment (examples from one participant). We calculated the spectral amplitude for the triple-related (left) and quadruple-related features (middle) and computed the difference (triple minus quadruple) to eliminate the effects of acoustic variability (right). **E.** Overall amplitude differences between triple-related and quadruple-related acoustic features across meter-related frequency bands. Each grey line represents individual data, whereas the bold black line indicates the average across participants. Positive values indicate stronger entrainment to triple-related features, whereas negative values indicate stronger entrainment to quadruple-related features. Asterisk (*) indicates a significant difference ($p_{Tukey} < 0.05$). **F.** Box plots and individual data of the band-specific amplitude difference between Bands 3 and 4. Greater values indicate stronger entrainment to triple-related features in Band-3 and weaker entrainment to quadruple-related features in the same band. The participants were classified into three groups in descending order: good (n = 11), middle (n = 12), and poor switchers (n = 11) for further analysis (see Fig. 3F-H).

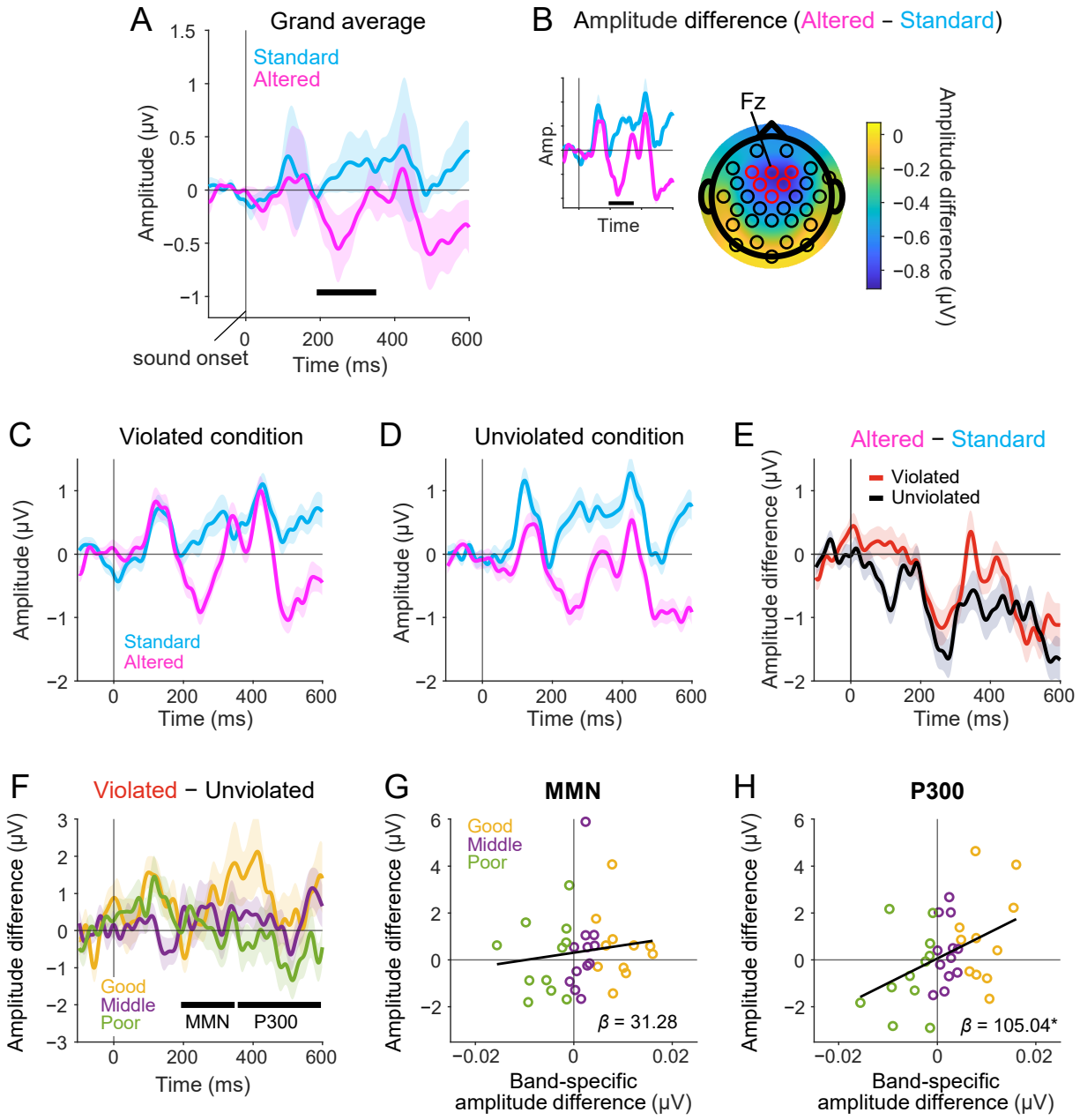

Fig. 3. Neural responses to metrical anticipation and their relationship with entrainment. A. Grand average of ERPs for standard and altered sounds, without categorizing violated and unviolated conditions. The shaded areas represent SD across the electrodes. **B.** The topographical electrode map of the amplitude difference (altered − standard) shows the largest difference at the Fz electrode. Consequently, Fz and its neighboring electrodes (F3, F4, FC1, FC2, and Cz, indicated by red circles) were selected for subsequent analysis. **C,D.** ERPs in the violated (C) and unviolated (D) conditions comparing standard and altered sounds. **E.** Amplitude differences (altered − standard sounds) under both conditions. **F.** The amplitude difference (violated − unviolated) across the three participant groups determined in the analysis of the band-specific amplitude difference (see Fig. 2F). We defined the time windows at 190-350 ms and 351-600 ms after the sound onset to assess MMN and P300, respectively. The shaded area in panels C–F represents the standard error across participants. **G,H.** Scatter plots showing the relationship between the band-specific amplitude difference and the amplitude difference (violated − unviolated) for the MMN (G) and P300 (H) time windows. Colored dots represent individuals in each participant group, and the β-value (slope) of the regression models is indicated. Asterisk (*) indicates a significant slope ($p < 0.05$).

Tables

Table1. Pairwise comparison of overall amplitude differences between meter-related frequency bands

Contrast	*Estimate* (10^{-3})	Lower 95% CI (10^{-3})	Upper 95% CI (10^{-3})	*t*-value	p_{Tukey}
Band-1 minus Band-2	–1.29	–3.91	1.34	−1.36	0.658
Band-1 minus Band-3	–3.44	–6.07	–0.81	−3.62	0.004*
Band-1 minus Band-4	–1.53	–4.16	1.10	−1.61	0.493
Band-1 minus Band-5	–0.95	–3.58	1.67	−1.00	0.853
Band-2 minus Band-3	–2.15	–4.78	0.47	−2.27	0.162
Band-2 minus Band-4	–0.24	–2.87	2.38	−0.26	1.000
Band-2 minus Band-5	0.33	–2.29	2.96	0.35	0.997
Band-3 minus Band-4	1.91	–0.72	4.54	2.01	0.266
Band-3 minus Band-5	2.49	–0.14	5.11	2.62	0.073
Band-4 minus Band-5	0.58	–2.05	3.20	0.61	0.974

Note: CI denotes confidence interval. $SE = 0.95 \times 10^{-3}$, $df = 132$, $*p_{Tukey} < 0.05$

Table 2. Linear regression model to examine the impact of band-specific amplitude differences on the amplitude difference (violated minus unviolated conditions) in the MMN time window.

Variable	*slope* [95%CI Lower, Upper]	*SE*	*t*-value	*p*-value
(Intercept)	0.31 [−0.28, 0.91]	0.29	1.08	0.290
Band-specific amplitude difference	31.28 [−51.07, 113.63]	40.43	0.77	0.445

Note: CI denotes confidence interval. F (1, 32) = 0.60, Adjusted $R^2 = -0.01$

Table 3. Linear regression model to examine the impact of band-specific amplitude differences on the amplitude difference (violated minus unviolated conditions) in the P300 time window.

Variable	*slope* [95%CI Lower, Upper]	*SE*	*t*-value	*p*-value
(Intercept)	0.07 [−0.51, 0.65]	0.29	0.25	0.807
Band-specific amplitude difference	105.04 [24.14, 185.94]	39.72	2.65	0.013*

Note: CI denotes confidence interval. F (1, 32) = 7.00, Adjusted $R^2 = 0.15$, $*p < 0.05$

Supplemental Information

Title:

Neural entrainment predicts the anticipatory P300 component during musical meter perception: An EEG study using dual-meter sound stimuli

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Text S1. Exploring the relationship between neural entrainment, anticipation, and behavioral sensitivity in detecting metrical violations.

To analyze the relationship between neural indices (entrainment and anticipation) and behavioral sensitivity to violations of metrical expectations, we conducted a supplemental behavioral analysis. After the EEG session, participants completed a task in which they judged whether an altered sound introduced a deviation when attending to either its center frequency or its duration. Each participant evaluated 28 stimuli per acoustic feature, resulting in 56 randomized trials. Participants had 2.5 s to respond and were instructed to answer as quickly and accurately as possible. If no responses were recorded, the next trial began automatically.

Sensitivity to metrical violations was quantified using the signal-detection theory (Gescheider, 1997). A hit was defined as the correct detection of a violation, whereas a miss indicated a failure to detect it. A false alarm referred to an incorrect report of a violation when none was present, and a correct rejection was an accurate identification of no violation. We define Z_N as the z-transformed value of (1 minus the proportion of false alarms), and Z_{SN} as the z-transformed value of (1 minus the proportion of hits). Detection accuracy (d') was calculated using the following equation:

$$d' = Z_N - Z_{SN} \quad \text{(Eq.S1)}$$

We then examined the relationship between d' (*mean* = 0.29, *SD* = 0.47) and three neural measures: (i) band-specific amplitude differences, (ii) amplitude differences (between the violated and unviolated conditions) during the mismatch-negativity (MMN) time window, and (iii) amplitude differences in the P300 time window. Because we had no predefined hypotheses about electrode locations, we computed the Pearson correlation coefficients without formal significance testing.

Stronger positive correlations between d' and band-specific amplitude differences were observed at F7 ($r = 0.38$), FC6 ($r = 0.32$), and FC5 ($r = 0.29$) (**Fig. S3A**). During the MMN window, the left hemisphere electrodes showed relatively strong negative correlations between d' and the amplitude difference at CP5 ($r = -0.30$), P3 ($r = -0.29$), and FC1 ($r = -0.25$) (**Fig. S3B**). In the P300 window, stronger positive correlations were observed in the right hemisphere electrodes such as FT10 ($r = 0.40$), PO10 ($r = 0.35$), and T8 ($r = 0.34$) (**Fig. S3C**). Therefore, these electrode sites may serve as promising targets for future studies investigating how neural indices of entrainment and anticipation relate to behavioral indices of meter violation detection.

References

Gescheider, G. A. (1997). *Psychophysics: The Fundamentals* (3rd ed.). Psychology Press.

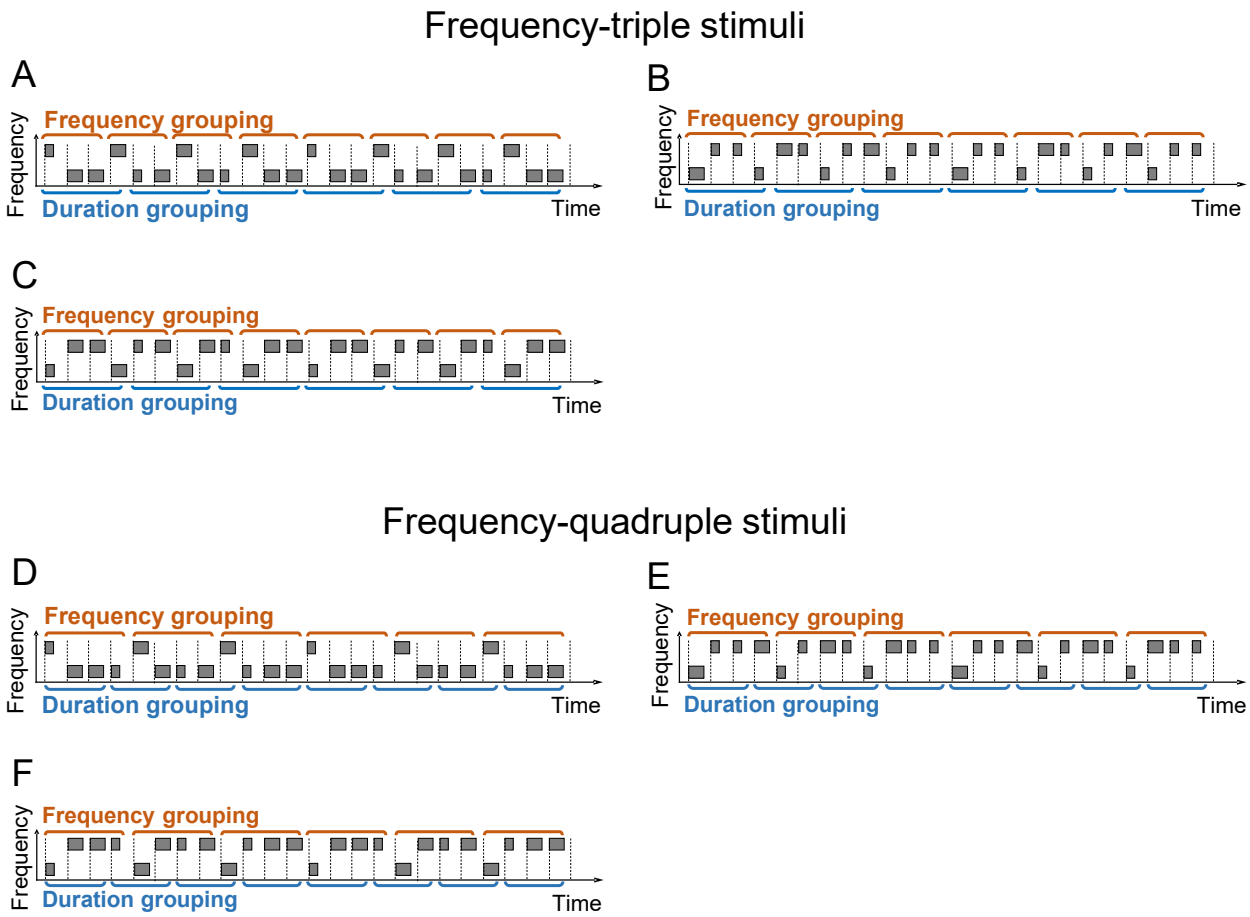

Fig. S1 Schematic representation of dual-meter stimuli not included in the main text. Each gray square represents a band-limited noise burst, with each stimulus consisting of 24 bursts. The center frequency of the higher sound was 1600 Hz and that of the lower sound was 1400 Hz, resulting in a frequency difference of 200 Hz. The duration of the longer sound was 150 ms, whereas that of the shorter sound was 50 ms, creating a duration difference of 100 ms. The bandwidth of each noise burst was set to 120% of its center frequency, and the inter-onset intervals (IOIs) were fixed at 300 ms. **A-C.** Frequency-triple stimuli. The frequency pattern is either "high–low–low–..." (panel A) or "low–high–high–..." (panels B and C), while the duration pattern follows either "short–long–long–long–..." (panels A and C) or "long–short–short–short–..." (panel B). **D-F.** Frequency-quadruple stimuli. The frequency pattern follows "high–low–low–low–..." (panel D) or "low–high–high–high–..." (panels E and F), while the duration pattern is either "short–long–long–..." (panels D and F) or "long–short–short–..." (panel E).

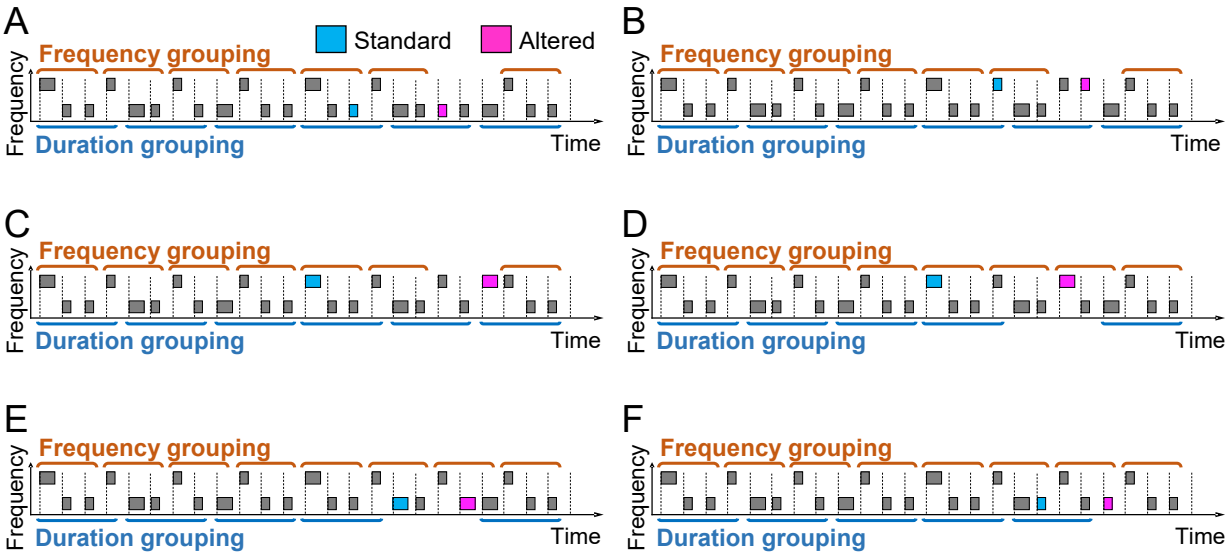

Fig. S2 Variations in one stimulus (Fig. 1A in the main text). Each pink square represents an altered sound, either by changing the center frequency of the 19th (panel A: high to low), 20th (panel B: low to high), or 21st (panel C: low to high) noise bursts or by changing the duration of the 19th (panel D: short to long), 20th (panel E: short to long), or 21st (panel F: long to short) noise bursts. For EEG analysis, standard sounds were defined as those that matched the altered sounds in both center frequency and duration and were presented at least three sounds ahead (indicated by light blue squares).

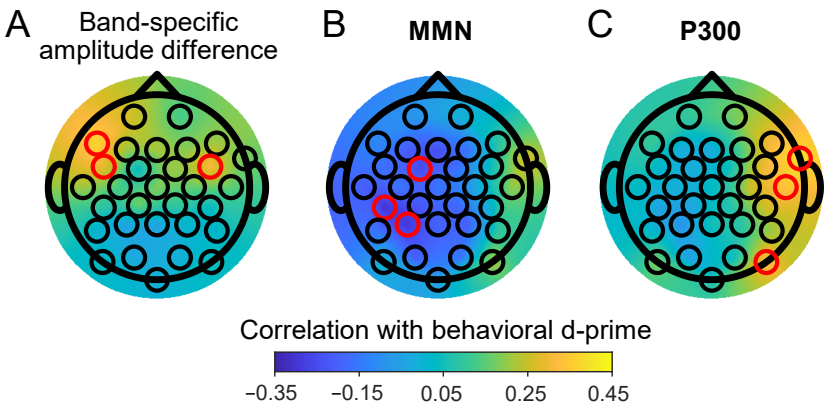

Fig. S3 Topographical distribution of correlations between behavioral d-prime (d') and EEG indices across the electrodes. A. Band-specific amplitude difference. The three electrodes (F7, FC5, and FC6, indicated by red circles) showed stronger positive correlations. **B.** Amplitude difference in the MMN time window. The three electrodes (CP5, P3, and FC1, indicated by red circles) exhibited stronger negative correlations. **C.** Amplitude difference in the P300 time window. The three electrodes (FT10, PO10, and T8, indicated by red circles) showed stronger positive correlations.