

## **RESEARCH REPORT**

## Alpha-Band Brain Activity Shapes Online Perceptual Learning of Concurrent Speech Differentially in Musicians vs. Nonmusicians

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### ABSTRACT

Plasticity from auditory experience shapes the brain's encoding and perception of sound. Though stronger neural entrainment (i.e., brain-to-acoustic synchronization) aids speech perception, underlying oscillatory activity may uniquely interact with long-term auditory experiences (i.e., music training) and short-term plasticity during concurrent speech perception. Here, we explored oscillatory activity during rapid auditory perceptual learning of concurrent speech sounds in normal-hearing young adults who differed in their amount of self-reported music training (defined as "musicians" and "nonmusicians"). Participants learned to identify double-vowel mixtures during ~45 min training sessions with concurrent high-density EEG recordings. We analyzed alpha-band power (7-12 Hz) following a rhythmic speech-stimulus train (~9 Hz) preceding behavioral identification to determine whether increased (brain-to-speech entrainment) or decreased alpha activity (alpha-band suppression) corresponded with task success. Source and directed functional connectivity analyses of EEG data probed whether behavior was driven by group differences in auditory-motor coupling. Both groups improved in behavioral identification with training. Listeners' alpha-band power prior to target speech predicted behavioral identification performance; surprisingly, stronger alpha oscillations were observed preceding incorrect compared to correct trial responses. We also found stark hemispheric biases in auditory-motor coupling, with greater auditory-motor connectivity in right compared to left hemisphere for musicians (R > L) but not in nonmusicians (R = L). Stronger alpha activity preceding incorrect behavioral responses supports the notion that alpha-band (~10 Hz) suppression is an important modulator of trial-by-trial success in perceptual processing. Our findings suggest that neural oscillations and auditory-motor connectivity interact with music training to impact speech perception.

Abbreviations: EEG, Electroencephalography; ERP, Event-related potential; FFR, Frequency-following response; GC, Granger causality; ISI, Inter-stimulus interval; LH, Left hemisphere; M, Musician; NM, Nonmusician; RH, Right hemisphere.

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## 1 | Introduction

Everyday listening involves complex auditory scenarios in which listeners must isolate information from one talker in the presence of other talkers and background noise. Though difficult, many listeners successfully navigate these types of "cocktail party" listening environments. In particular, an extensive body of literature demonstrates perceptual advantages in speech-in-noise and "cocktail party" listening among highly-trained musicians (Bidelman and Yoo 2020; Maillard et al. 2023; Parbery-Clark, Skoe, and Kraus 2009; Puschmann et al. 2018; Zendel and Alain 2009). Despite evidence for a musician speech-in-noise advantage, the exact mechanism(s) underlying these enhancements are still debated. Enhanced sensory processing (Bidelman et al. 2011; Koelsch et al. 1999; Strait et al. 2010), attention (Román-Caballero et al. 2020; Strait and Kraus 2011), and working memory/executive function (Kraus et al. 2012; Pallesen et al. 2010; Zuk et al. 2014) all might explain musicians' superior figure-ground speech perception abilities.

One potential mechanism that might enhance auditory perception, including noise-degraded and concurrent speech perception, is neural entrainment. Neural entrainment, or the yoking of ongoing neural oscillations to external stimuli, plays a strong role in governing the perceptual parsing of speech (Vanthornhout et al. 2018) and musical sounds (Doelling et al. 2019). Entraining to speech facilitates its intelligibility both in quiet and noise (Riecke et al. 2018). On the contrary, electrophysiological studies have shown that poorer entrainment in clinical populations (e.g., listeners with auditory processing disorder) parallels behavioral deficits in concurrent speech listening tasks (Gilley et al. 2016; Momtaz et al. 2021, 2022). Collectively, these studies suggest the robustness of the brain's neuroacoustic entrainment might play an important role in successfully parsing concurrent speech signals.

An alternative idea is that changes in intrinsic rhythmic oscillatory power of brain activity might underly task performance. Increases in alpha-band (7–12 Hz) brain rhythms are traditionally associated with internal reflection or decreased attention to a given task (Klimesch 2012). Related to task performance, phase-related changes and *suppression* of alpha activity have been shown to predict successful speech intelligibility in quiet and noise (Obleser et al. 2012; Strauß et al. 2015; Weisz et al. 2011). Cortical alpha states also influence brainstem speech encoding through dynamic fluctuations in arousal and attention, and consequently, are relevant to speech processing at multiple stages of the auditory system (Lai et al. 2022). Thus, it is also possible that reduced alphaband activity could support improved task performance in speech perception tasks.

Aside from entrained or endogenous alpha activity, brainto-brain interactions between the auditory and motor systems might also aid the perception of "cocktail party" speech. Previous studies have demonstrated engagement of the motor system (alongside the auditory system) to enhance the neural representation of speech (Poeppel and Assaneo 2020; Poeppel and Hickok 2004). Indeed, close coordination between the premotor and temporal cortices is used to track various linguistic elements of the speech signal spanning the syllable, word, and phrase levels (Assaneo and Poeppel 2018; Ding et al. 2016; He et al. 2023; Keitel et al. 2018). Motor engagement is particularly evident under noise degradation when efference copy must enhance speech representations from the impoverished acoustic input (Du et al. 2014). Such top-down, cross-modal enhancement of auditory information might also be due to the ability of the motor system to enhance temporal predictions of sensory stimuli (Dick et al. 2011; Morillon and Baillet 2017). These mechanisms could presumably improve degraded listening skills. One idea is that the enhanced auditory-motor integration necessary for musicians may enhance auditory-motor connectivity, thus enabling their more successful speech-in-noise comprehension (e.g., Du and Zatorre 2017).

Functional connectivity between the auditory and motor systems (i.e., the degree of coupling between regional activity) can directly characterize auditory-motor signaling. Germane to our current study, Puschmann and colleagues found that when attending to continuous speech in quiet, the amount of participants' music training positively correlated with the strength of alpha-band phase locking between the primary auditory cortex and dorsal and ventral auditory pathways, suggesting alpha-band entrainment to speech across the cortex is influenced by music training (Puschmann et al. 2021). Functional connectivity enhancements associated with musicianship may even align with prevention of typical age-related declines in speech-in-noise perception (Zhang et al. 2024). In addition to connectivity strength, the direction of signaling (i.e., auditory-to-motor vs. motor-to-auditory) can provide insight into "bottom up" vs. "top-down" mechanisms of auditory-motor involvement. Stronger connectivity in the auditory-to-motor direction could indicate greater reliance on sensory cue extraction and specific stimulus features, whereas stronger motor-to-auditory signaling could indicate greater reliance on predictive or anticipatory cues to perceive cocktail party speech.

In the present study, we reanalyzed EEG data collected in our previously published, cross-sectional study on the neuroplasticity of concurrent speech sound learning in musicians and nonmusicians, individuals who self-reported high and low amounts of music training, respectively (MacLean et al. 2024). In that work, we found that long-term plasticity (e.g., musicianship) interacted with short-term perceptual learning (e.g., learning a task within one ~45 min session) in the perception of double-vowel speech stimuli. Musicians and nonmusicians demonstrated different neurophysiological responses and learning trajectories which related to behavioral measures of speech identification. Fortuitously, our stimulus design included a rapid cueing speech train at the nominal alpha-band frequency (~10 Hz). This allowed us to now investigate alpha power during and after stimulus presentation to determine how the directionality in alpha activity predicts speech identification at the single trial level. Under a neural entrainment hypothesis (Riecke et al. 2018), we expected increased alpha responses phase-locked to the 10 Hz speech rhythm would predict better task performance. In contrast, the alpha suppression hypothesis predicts decreased alpha prior to behavioral decision should correlate with better



**FIGURE 1** | Clustered stimulus paradigm to induce alpha-band speech entrainment. The stimulus paradigm began with a rapid stimulus train presented at ~10 Hz, followed by a 1100 ms period of silence before the isolated vowel pair which cued behavioral responses (Bidelman 2015). Analyses were performed on induced neural entrainment observed during the silent period.

perception. In sum, our findings show that alpha-band oscillations dramatically increase during incorrect but not correct trials (especially in musicians) and are therefore most consistent with a suppression hypothesis, whereby downregulating alpha rhythms during perceptual processing is important for task success. Our findings also reveal nuanced differences in auditory-motor functional connectivity based on differences in self-reported music training.

## 2 | Materials and Methods

The current study represents a new analysis of neural oscillations from the EEG data reported in MacLean et al. (2024). Evoked potential results including brainstem (frequencyfollowing response, FFR) and cortical (event-related potential, ERP) responses to speech and how they are modulated by perceptual learning are reported in the companion paper (MacLean et al. 2024). The reader is referred to the original manuscript for full methodological details.

## 2.1 | Participants

Twenty-seven young adults (ages 18-34; mean + SD 23.68 + 4.22; 13 female) with normal hearing thresholds (bilateral pure tone averages < 25 dB HL, octave frequencies between 250 and 8000 Hz) participated in this study. All participants were fluent in American English and reported no previous neurologic or psychiatric disorders. Participants gave written, informed consent in accordance with a protocol approved by the Indiana University Institutional Review Board.

Participants were separated into musician (M; n=13) and nonmusician (NM; n=14) groups based on their extent of selfreported formal music training (hereafter referred to as "musicians" and "nonmusicians"). Musicians had at least 10years of self-reported formal music training starting at or before age 12, while nonmusicians had 5 or fewer years of lifetime music training (Wong et al. 2007). Groups did significantly differ in amount of music training (M 16.1 + 4.3 years; NM 2.4 + 1.7 years; t(25)=10.93; p<0.001) but were matched in age (t(25)=1.58; p=0.413), cognitive ability as assessed through the Montreal Cognitive Assessment (Nasreddine et al. 2005) (t(25)=1.78; p=0.088), self-reported bilingualism ( $X^2(1, N=27)=0.022$ , p=0.883), sex balance ( $X^2(1, N=27)=1.78$ , p=0.182), and handedness as assessed through the Edinburgh Handedness Inventory (t(25) = -0.615; p = 0.544) (Oldfield 1971).

#### 2.2 | Double-Vowel Stimuli and Task

Concurrent vowel stimuli were modelled after previous studies (Alain et al. 2007; Assmann and Summerfield 1989, 1990; Bidelman and Yellamsetty 2017). Stimuli consisted of synthesized, steady-state vowels (/a/, /e/, and /i/) which were presented in three unique vowel combinations (i.e., /a/ + |e|; |e| + |i|; |a| + |i|). Vowels were never paired with themselves. Stimuli were created with a Klatt-based synthesizer (Klatt 1980) coded in MATLAB (v 2021; The MathWorks, Inc., Natick, MA). Each vowel was 100 ms in duration with 10-ms cos<sup>2</sup> onset/offset ramping to prevent spectral splatter. The fundamental frequency (F0) between vowels was 4 semitones (150 and 190 Hz), which promotes segregation for most listeners (Assmann and Summerfield 1990; Bidelman and Yellamsetty 2017). F0 and the first two formant frequencies (F1<sub>a.e.i</sub>=787, 583, 300 Hz; F2<sub>a.e.i</sub>=1307, 1753, 2805 Hz) remained constant for the duration of the token.

The speech sounds were presented in rarefaction phase through a TDT RZ6 interface (Tucker-Davis Technologies, Alachua, FL) controlled via MATLAB. Stimuli were presented binaurally at 79dB SPL through electromagnetically shielded (Campbell et al. 2012; Price and Bidelman 2021) ER-2 insert earphones (Etymotic Research, Elk Grove, IL). Prior to EEG testing, we required all participants to identify single vowels with 100% accuracy. This ensured subsequent learning would be based on improvements in *concurrent* speech identification rather than isolated sound labeling ability.

We used a clustered stimulus paradigm (Bidelman 2015) employing interspersed fast and slow interstimulus intervals (ISIs) to collect speech-evoked potentials during the active perceptual task (Figure 1). Speech-ERP/FFR data are reported in the companion paper (MacLean et al. 2024). Each trial consisted of one of the three vowel combinations. During a trial, 20 repetitions of the vowel pair were presented with a fast ISI of 10 ms to elicit the FFR. Thus, the corresponding stimulus onset asynchrony was 110 ms (i.e., 9.09 Hz). The ISI was then slowed to 1100 ms and a single stimulus was presented to evoke the ERP and cue a behavioral response. Participants then identified both vowels through keyboard responses following the isolated vowel pair. The next trial began after the participants' response and 250 ms of silence. Participants were asked to identify both vowels as quickly and accurately as possible (no feedback was provided), and accuracy (defined as percentage of responses where both vowels were correctly identified) and reaction time (RT) were recorded for each trial. Double vowel pairs were randomized in order. This identical task was repeated over four learning blocks. In total, each block included 150 stimulus trials. Each block took 10–15 min to complete. Participants were offered a short (2–3 min) break after each block to avoid fatigue.

To investigate alpha activity induced by the preceding speech stimuli prior to listeners' behavioral response, we isolated neural activity to the stimulus train (-3300 to -1100 ms) and subsequent silent period (-1100 to 0 ms) just prior to target presentation that probed listeners' speech identification. This allowed us to assess how ongoing brain rhythms respond to rhythmic speech stimulation and consequently modulate success in identification.

## 2.3 | EEG Recording and Preprocessing

We used Curry 9 (Compumedics Neuroscan, Charlotte, NC) and BESA Research 7.1 (BESA, GmbH) to record and preprocess the continuous EEG data. Continuous EEGs were acquired from 64-channel Ag/AgCl electrodes positioned at 10-10 scalp locations (Oostenveld and Praamstra 2001). Recordings were digitized at 5kHz using Neuroscan Synamps RT amplifiers. Data were referenced to an electrode placed 1cm behind Cz during online recording. Data were re-referenced to common average reference for subsequent analysis. Impedances were kept below 25 k $\Omega$ . Electrodes placed on the outer canthi of the eyes and superior and inferior orbit captured ocular movements. Eyeblinks were corrected using a topographic principal component analysis (Wallstrom et al. 2004). Responses were collapsed across vowel pairs to obtain an adequate number of trials for analysis (Bidelman and Yellamsetty 2017; Yellamsetty and Bidelman 2018). Responses exceeding 150 µV were rejected as further artifacts. We then bandpass filtered responses from 7 to 12 Hz (zero-phase Butterworth filters; slope = 48 dB/octave) to isolate alpha-band activity (Alain et al. 2023; Bidelman 2017; Lai et al. 2022), corresponding to the nominal rate of our speech train stimuli. Data were then epoched during the train (-3500 to -1100 ms) and silent portions of the stimulus presentation (-1100 to 0 ms) separately, baselined, and ensemble averaged to derive sustained response waveforms for each condition per subject. For subsequent analyses, neural responses were separated by listeners' trial-by-trial response accuracy (correct vs. incorrect trials).

#### 2.4 | Fast Fourier Transforms

To measure the strength of oscillatory activity influenced by the rapid stimulus train, we computed the Fast Fourier Transform (FFT) in the -3500 to -1100 (train) and -1100 to 0 ms (silence) time windows separately for each block and correct/incorrect trials. We measured the magnitude and frequency for the maximum spectral peak within the alpha band (7–12 Hz) at the Cz electrode to quantify alpha activity at the scalp level.

## 2.5 | Functional Connectivity

To resolve the underlying brain sources of entrainment effects, we measured directional flow of information within the auditory-motor network using Granger Causality (GC) (Geweke 1982; Granger 1969). GC measures the degree to which Signal A "Granger-causes" Signal B and is computed directionally in order to infer causal flow of information between brain regions. We computed functional connectivity in the frequency domain between primary auditory (A1) and motor (M1) cortex sources, bilaterally, using BESA Connectivity (v2.0) (Dhamala et al. 2008; Geweke 1982). A1 and M1 region of interest (ROI) source locations were defined via Talairach coordinates in template brain space (x, y, z coords.: M1:  $\pm 44.8$ , -7.8, 38.24 cm; A1:  $\pm$ 50.4, -21.7, 11.5 cm). Frequency decomposition was based on complex demodulation (Papp and Ktonas 1977), which results in uniform frequency resolution across the analysis bandwidth (i.e., sliding window FFT). The time-frequency analysis initially spanned the entire epoch window (-3400 to 1000 ms), using a pre-stimulus baseline (-3400 to -3200 ms) over a bandwidth between 5–20 Hz (i.e., centered at the nominal alpha frequency). However, we extracted GC within the post-stimulus train silence (-1100 to 0 ms) within the 7-12 Hz band (collapsed across time and frequency) to examine alpha auditory motor coupling just prior to the target cue and behavioral decision. We computed GC between A1 and M1 in both the forward and reverse directions  $(A1 \rightarrow M1 \text{ and } M1 \rightarrow A1, \text{ respectively})$  to assess directed "bottom-up" and "top-down" neural signaling between auditory and motor system.

## 2.6 | Statistical Analyses

Unless otherwise noted, we analyzed dependent variables using mixed model ANOVAs in R (version 4.2.2) (R-Core-Team 2020) using the lme4 package (Bates et al. 2015). Behavioral measures (accuracy, RT) were analyzed with fixed effects of group (2 levels) and block (4 levels) and random effect of subject, with an additional fixed effect of behavioral response (2 levels, correct or incorrect) for RTs. Oscillatory strength was analyzed with fixed effects of group (2 levels), block (4 levels), behavioral response (2 levels), and random effect of subject separately for the train and silent portions of the stimulus. Additionally, we included a covariate for the number of trial counts for correct and incorrect responses. Granger Connectivity was analyzed with the same fixed and random effects as above, with two additional fixed effects of hemisphere (2 levels; left vs. right) and direction (2 levels; forward:  $A1 \rightarrow M1$ , reverse:  $M1 \rightarrow A1$ ). Effect sizes are reported as partial eta squared  $(\eta_p^2)$  and degrees of freedom (d.f.) using Satterthwaite's method. Multiple pairwise comparisons were adjusted using Tukey method. Linear contrasts were adjusted using the Sidak method.

Initial diagnostics indicated heavy tailed distributions for both neural measures. Consequently, we used the Box–Cox procedure (Box and Cox 1964) to transform the data and satisfy normality assumptions necessary for parametric statistics. This procedure transforms the data according to  $y' = (y^{\lambda} - 1)/\lambda$ , where  $\lambda = 0.071$  and  $\lambda = -0.11$  where determined empirically for oscillatory strength and connectivity, respectively.

#### 3 | Results

#### 3.1 | Behavior

Figure 2 displays behavioral results for accuracy and reaction time (RT) for both M and NM groups across all four training blocks. An ANOVA on behavioral accuracy revealed a main effect of training block [F(3, 75)=12.13, p < 0.001,  $\eta_p^2 = 0.33$ ]. Both groups improved in accuracy with training block (linear contrast:M: t(75)=4.34, p < 0.001; NM: t(75)=3.01, p=0.0035). The ANOVA on RT revealed an interaction between group and response accuracy [F(1, 171.59)=7.68, p=0.0062,  $\eta_p^2 = 0.04$ ] driven by faster RTs for musicians during correct trials only (pairwise comparison: correct t(35.9)=-1.89, p=0.067; incorrect t(35.7)=0.43, p=0.67). A main effect of block was also observed on RT [F(3, 171.44)=14.91, p < 0.0001,  $\eta_p^2 = 0.21$ ] driven by decreasing RT with block for both groups (linear contrast: t(171)=-5.65, p < 0.0001).



**FIGURE 2** | Behavioral accuracy and reaction time improved with training block. Behavioral measures are shown separately for correct and incorrect trials. (a) Accuracy in identifying both concurrently presented vowels improved with training block for both musicians and nonmusicians. Dashed line represents chance performance level. (b) Reaction time decreased with training block, with musicians exhibiting faster reaction times for correct trials. Boxes represent the middle 50% of each distribution, whiskers extend to 1.5 multiples of the interquartile range.

# 3.2 | Oscillatory Activity During Stimulus Train and Silent Periods

Figure 3 displays alpha-band waveforms during the entire stimulus period. We analyzed alpha-band strength during the rapid stimulus train and silent portions of the stimulus period separately. Due to similar results for both stimulus portions, for subsequent connectivity analyses, we focused on the silent period just prior to the target double-vowel presentation that cued listeners' behavioral response to assess ongoing oscillatory activity without the presence of external stimulation.

Figure 4 shows alpha-band entrainment amplitude in the rapid train (Figure 4a) and silent (Figure 4b) periods (i.e., just prior to the target cue) for correct and incorrect trials. Visually, the frequency specificity of the stimulus train can be seen in the sharper ~10 Hz peak for the train compared to the silence FFTs. The added broadening of the FFTs for the silent period and incorrect trials likely reflects on overlay of intrinsic alpha oscillations on top of the phase-locked activity evoked by the 10 Hz stimulus rhythm.

An ANOVA on alpha-band amplitude during the stimulus train revealed a group x block interaction [F(1, 172.38) = 3.40, p = 0.019,  $\eta_p^2 = 0.06$ ], driven by increasing amplitude with block for musicians only (linear contrast: M: t(178) = 3.67, p = 0.001; NM: t(174) = -0.43, p = 0.96). We also observed a group × response accuracy interaction [F(1, 172.38) = 4.91, p = 0.028,  $\eta_p^2 = 0.03$ ], driven by musicians' stronger amplitudes preceding incorrect trials compared to nonmusicians [t(27.8) = 1.81, p = 0.080].

During the silent period, we observed a two-way interaction between group x trial accuracy  $[F(1, 172.38) = 4.52, p = 0.035, \eta_p^2 = 0.03]$  (Figure 4c), driven by larger spectral amplitudes for musicians than nonmusicians preceding incorrect trials [t(29) = 2.20, p = 0.036]. Groups showed similar response amplitudes before correct trials [t(29) = 1.011, p = 0.32]. There was also a block x response accuracy interaction  $[F(3, 172.38) = 4.014, p = 0.0086, \eta_p^2 = 0.07]$ . A linear contrast revealed this interaction was due to a steady increase in response amplitude across blocks for incorrect trials [t(177) = 4.18, p < 0.0001], regardless of group. Responses were invariant across blocks for correct trials [t(177) = -0.41, p = 0.68]. A post-hoc Pearson correlation revealed that alpha-band amplitude during stimulus silence was not correlated with RT for



**FIGURE 3** | Alpha-band responses during the stimulus time course. Alpha-band (7–12Hz) waveforms for musicians and nonmusicians preceding correct (a) and incorrect (b) behavioral responses. Gray boxes represent stimulus in the rapid stimulus train (see Figure 1). Analyses were performed during the silent portion of the stimulus paradigm (yellow) just prior to the behavior-cueing token at t=0 (black box).



**FIGURE 4** | Alpha oscillations following a rapid speech stimulus train predicts subsequent behavioral identification accuracy for double-vowel mixtures. (a) FFTs are displayed for musicians and nonmusicians during stimulus trains preceding correct and incorrect trials. Insets show time waveforms of the post-train period (see yellow shading, Figure 3). (b) FFTs are displayed during the silent stimulus period. Visually, the specificity of the stimulus train can be seen in a sharper peak for the train FFTs compared to the wider silence FFTs. (c) Musicians had stronger alpha band responses during silent intervals preceding incorrect trials than did nonmusicians, despite similar responses preceding correct trials. Results were similar for responses during the stimulus train. Boxes represent the middle 50% of each distribution, whiskers extend to 1.5 multiples of the interquartile range.

correct (r = -0.041, p = 0.68) nor incorrect (r = -0.11, p = 0.29) trials.

## 3.3 | Auditory-Motor Connectivity

Figure 5 depicts time-frequency plots of source-level waveforms from auditory (A1) and motor (M1) cortex in the left (LH) and right hemispheres (RH) per group. Spectrographic maps were used to calculate GC connectivity, reflecting directed neural signaling between ROIs, for correct and incorrect trials per hemisphere and group (Figure 6).

A mixed-model ANOVA on GC strength revealed several two-way interactions (Figure 7). We found an interaction between hemisphere and group (Figure 7a) [F(1, 766.72) = 9.07,p = 0.0027,  $\eta_p^2 = 0.01$ ]. This was driven by stronger GC values in the right hemisphere compared to the left hemisphere for musicians only (pairwise comparison: M: t(766) = -4.69, p < 0.0001, NM: t(766) = -0.555, p = 0.58). An interaction between group and block (Figure 7b) [F(3, 769.72) = 3.64,p = 0.013,  $\eta_n^2 = 0.01$ ] was driven by greater connectivity with block for musicians only (linear contrast: M: t(791) = 3.16, p = 0.0050; NM: t(779) = 1.51, p = 0.35). We also observed an interaction between group and response accuracy (Figure 7c)  $[F(1, 766.72) = 5.030, p = 0.025, \eta_p^2 < 0.01]$  which was driven by stronger GC during incorrect trials in both groups but especially musicians (pairwise comparison: M: t(766) = -13.69, p < 0.0001; NM: t(766) = -11.11, p < 0.0001). Finally, an interaction between block and response accuracy (Figure 7d)  $[F(3, 766.72) = 4.55, p = 0.0036, \eta_p^2 = 0.02]$  was driven by increasing connectivity with block for incorrect trials only (linear contrast: correct: t(787) = 0.12, p = 0.99; incorrect:

t(787) = 4.60, p < 0.0001). All other interactions were nonsignificant. Additionally, we observed a main effect of direction (Figure 7e) [ $F(1, 766.72) = 4.53, p = 0.034, \eta_p^2 < 0.01$ ], attributed to higher auditory-to-motor (i.e., A1  $\rightarrow$  M1) compared with motor-to-auditory (i.e., M1  $\rightarrow$  A1) connectivity in both groups.

#### 4 | Discussion

By analyzing EEG oscillatory activity during perceptual learning of double-vowel mixtures in musicians and nonmusicians, we found (i) stronger alpha-band power preceding incorrect responses, especially for musicians; (ii) greater learning-related changes in connectivity for musicians, especially in the right hemisphere and preceding incorrect responses; and (iii) stronger bottom-up (auditory-to-motor) than top-down (motor-toauditory) connectivity for both groups.

#### 4.1 | Musicians Show Stronger Modulation of Alpha Activity That Varied With Trial Success

Individuals with higher amounts of self-reported music training (musicians) had stronger alpha-band (7–12Hz) activity preceding incorrect trials in our double-vowel identification task than individuals with lower amounts of self-reported music training (nonmusicians). As our stimulus train (~9Hz) overlaps with the alpha range, increased alpha activity could indicate stronger persistent stimulus entrainment after the sound has stopped (entrainment hypothesis) (Riecke et al. 2018) or *reduced* outward attention to the stimulus and greater inward reflective processing (alpha-suppression hypothesis) (Klimesch 2012). Given that increased alpha activity was associated with incorrect rather



**FIGURE 5** | Source time-frequency responses reflecting neural activity within the auditory-motor network. Each spectrogram demonstrates spectral density within the alpha band range stemming from auditory (A1) and motor (M1) cortex. Hot colors, %-increase in activity relative to baseline; cool colors, %-decrease activity. t=0 denotes the onset of the double-vowel mixture that cued listeners' behavioral response. Note the power at ~10Hz reflecting phase-locking to the rapid stimulus train (see Figure 1a) which is also stronger in musicians. L/R = left/right hemisphere.

than correct responses, our data favor the suppression account of alpha-band rhythms. One potential explanation for increased activity associated with reduced attention to task is that larger alpha power reflects decreased neuronal excitability (e.g., inhibition), which leads to reduced stimulus encoding at the sensory level. As a result of diminished stimulus encoding, task performance becomes poorer (Iemi et al. 2022). Increases in alpha activity after the rhythmic speech stimulus and before target cue could indicate that participants were "tuning out" the trial and therefore responded incorrectly (Klimesch 2012).

Trial-dependent changes in alpha power were stronger for musicians than nonmusicians preceding incorrect trials, despite similar levels of activity between groups preceding correct responses. One explanation for this finding could be that musicians are greater "modulators" of alpha brain rhythms. Previous studies have shown that changes in alpha oscillations are associated with improved task performance (Klimesch 2012; Lai et al. 2022; Pfurtscheller and Lopes da Silva 1999; Price et al. 2019; Strauß et al. 2015). We have also recently demonstrated listeners who show less stimulusrelated changes in their alpha (i.e., "low alpha modulators") achieve poorer performance on speech-in-noise perception tasks (Price et al. 2019). Alpha desynchronization in sensory, task-relevant brain areas may even be paired with alpha synchronization over task-irrelevant areas where inhibition is necessary (Mazaheri et al. 2014). Alpha power is also associated with attentional biasing during auditory processing, including tasks involving the perception of difficult and ambiguous speech (Alain et al. 2023). Greater alpha activity preceding incorrect trials may thus reflect changes in task-related inhibition and/or attentional gating. Indeed, broad increase in pre-stimulus neural activation predicts speech recognition errors (Vaden et al. 2015, 2022). And consistent with our electrophysiological data, alpha power can be stronger preceding incorrect responses (Samaha et al. 2020). Regardless of the mechanistic interpretation of alpha waves, it is clear musicians recruit greater changes in alpha power between successful and unsuccessful trials (Figure 4b). Given musicians' faster performance in double-vowel identification (MacLean et al. 2024), it would appear that a more dynamic alpha-band activation is advantageous for neuro-perceptual processing. A wider range of alpha control could also explain musicians' greater flexibility in deploying attentional resources during speech perception (Strait and Kraus 2011). This notion converges with previous findings showing that acoustic-phonetic properties of speech indexed by alpha rhythms are amplified in musicians and support more robust categorization in speech perception tasks (Bidelman 2017).

Relatedly, under the canonical attentional interpretation of alpha, increased alpha activity in musicians may be the result of greater "tuning-out," or reduced attentional gating to the task during incorrect trials. In this vein, EEG alpha activity is



**FIGURE 6** | Auditory-motor coupling varies by group, hemisphere, and trial-wise accuracy. Granger connectivity values were strongest for musicians in the right hemisphere preceding incorrect trials. Both groups had weaker connectivity in the motor to auditory direction. Boxes represent the middle 50% of each distribution, whiskers extend to 1.5 multiples of the interquartile range.



**FIGURE 7** | Significant interactions and main effects on Granger connectivity. (a) Hemisphere  $\times$  group, (b) block  $\times$  group interaction, (c) group  $\times$  response accuracy, and (d) block  $\times$  response accuracy interactions. (e) Main effect of direction. Connectivity was stronger in the auditory-motor (bottom-up) vs. motor-auditory (top-down) direction. Boxes represent the middle 50% of each distribution, whiskers extend to 1.5 multiples of the interquartile range.

associated with GABAergic neuronal processing that is linked to intrinsic brain activity and suppressing task-irrelevant information (Klimesch et al. 2007). It is possible that the task was easier for musicians. Reduced attention to the task would account for the greater engagement of alpha-band activity we find in musicians, especially preceding incorrect responses. Though, we note musicians showed faster decision speeds in double-vowel identification in correct (but not incorrect) trials, ruling out a blanket attentional lapse interpretation of our data. Musicians' greater alpha desynchronization for successful trials could reflect stronger attentional modulation or even greater resources for redirecting attention when needed (or desired). Indeed, both groups showed increased behavioral performance with block, but musicians exhibited faster RTs for correct-only trials than nonmusicians. Thus, it is conceivable that performance may have become more automatized in musicians during the time course of learning. This is additionally supported by our functional connectivity data. Musicians showed increased alpha-band auditory-motor connectivity with training block, whereas nonmusicians did not. In this vein, prior studies have shown greater selective auditory attention for musicians in concurrent speech or "cocktail party" scenarios (Brown and Bidelman 2023; Clayton et al. 2016; Strait et al. 2010), but see (Baumann et al. 2008), and there is also evidence that inhibitory attentional control is stronger and more efficient in musically trained individuals (Medina and Barraza 2019).

Further support for interpretation of increased alpha power as reduced attention to task is supported by findings relating alpha power to creativity (Stevens and Zabelina 2019). Similarly, greater auditory-motor connectivity for musicians preceding incorrect trials may be the result of increased internal reflection. Reflective processing coincides with decreased arousal/attention observed through alpha desynchronization (Klimesch 2012). Internal reflections or "daydreaming" prior to incorrect trials could indicate more widespread, inefficient processing unrelated to the task (Fink and Benedek 2014). Previous studies link stronger alpha activity and resting-state functional connectivity with creativity in long-term trait (Bazanova and Aftanas 2008; Beaty et al. 2014) and short-term task-related (Stevens and Zabelina 2019) contexts. Understanding increased alpha activity as reduced attention to task goes hand in hand with greater "tuning out" or internal reflection, though our task did not measure this phenomenon explicitly.

Determining the facilitatory or inhibitory role of alpha in concurrent speech listening, as well as how this role may be modulated by music training, could inform future interventions to improve everyday complex listening skills (Gray et al. 2022). For example, the overall power and ability to modulate alpha activity to suppress irrelevant information declines in older listeners, which may render pre-target oscillations weaker and less viable as a mechanism for attentional gating (Klimesch 1999; Vaden et al. 2012; Wöstmann et al. 2015). As implied by prior behavioral and neuroimaging studies, music engagement might help offset these age-related declines in auditory processing and help fortify the sensoryattentional mechanisms necessary for parsing complex speech mixtures (Bidelman and Alain 2015; Lu et al. 2022; Zendel and Alain 2009, 2012; Zendel et al. 2019). Our study only examined alpha activity following a cueing rhythmic speech train in the alpha range. Further exploration of the role of such induced (endogenous) alpha entrainment, both to external speech and between brain areas, and how it interacts with stimulus-related speech phase-locking (Puschmann et al. 2018) is needed in order to understand neuroplastic changes in oscillatory activity and how it benefits concurrent speech perception. In this vein, neurostimulation studies have already demonstrated that enhancing cortical entrainment causally improves comprehension including performance for noise-degraded speech (Guilleminot and Reichenbach 2022; Wilsch et al. 2018).

## 4.2 | Auditory-Motor Connectivity During Concurrent Speech Listening Differs Based on Musicianship

During our active double-vowel perception task, musicians showed greater auditory-motor connectivity in the right hemisphere, whereas nonmusicians displayed similar connectivity in both hemispheres. These results are in line with emerging findings suggesting musicianship is associated with stronger functional connectivity in the right hemisphere that is associated with preserved speech-in-noise capabilities with age (Zhang et al. 2024). Right hemispheric brain pathways are dominant for pitch and fine spectral processing (Zatorre et al. 2002, 1992). Thus, greater RH engagement in musicians may indicate their greater "cue-weighting" of pitch-based cues to distinguish vowels during our concurrent speech task, in line with our previous ERP findings of the same data (MacLean et al. 2024). Relatedly, other studies suggest that musicians have stronger right hemisphere entrainment to speech within the alpha band (Puschmann et al. 2021). Nonmusicians' similar patterns of connectivity between left and right hemispheres may indicate that neither a leftbiased linguistic (Hickok and Poeppel 2007; Mankel et al. 2022) nor right-biased pitch strategy was preferred. Given musicians' greater speed in the task (MacLean et al. 2024), a pitch-based, spectral strategy may have been advantageous which could explain the larger recruitment of RH activity observed in our data.

## 4.3 | Auditory-Motor Connectivity Is Stronger in the Bottom-Up vs. Top-Down Direction

We found both musicians and nonmusicians had stronger connectivity in the auditory-to-motor compared to motor-toauditory direction prior to double-vowel identification. The directionality of connectivity provides insight as to whether concurrent speech stimuli were processed in a bottom-up (auditoryto-motor) or top-down (motor-to-auditory) manner. Here, greater auditory-motor connectivity preceding behavior may indicate more reliance on the extraction of stimulus-specific features than anticipatory motor representations of the speech stimuli (Morillon and Baillet 2017; Tian and Poeppel 2012). One idea is that the motor system becomes involved in speech perception when listening becomes difficult, such as when acoustic input is sparse (Osnes et al. 2011) or speech is presented in noise (Du et al. 2016). As we observed stronger bottom-up connectivity for both groups, stimulus-based feature extraction may be more advantageous than anticipatory timing during our task. That is, the repetitive stimulus train and simultaneous onset for both vowels may have decreased the need for reliance on top-down anticipatory motor-system strategies (Wu et al. 2014). Alternatively, if the task became more automatic with learning, this would tend to evoke more bottom-up signaling, which is also enhanced in musicians (Bidelman and Krishnan 2010; Bidelman et al. 2014; Musacchia et al. 2007; Parbery-Clark, Skoe, and Kraus 2009; Puschmann et al. 2018). Our stimulus train was also periodic and predictable. It is possible that changes to the timing and/or predictability of speech sounds (e.g., jittered stimulus train) may differentially recruit auditory-motor engagement and alter the direction of connectivity during speech processing (cf. Momtaz and Bidelman 2024; Morillon and Baillet 2017). Future studies are needed to test these possibilities.

## 4.4 | Limitations

Though many studies (including the present) have demonstrated biobehavioral "musician advantages" in speech perception tasks, we would be remiss to not acknowledge the cross-sectional nature of our study. As such, we are not able to tease apart effects of music training from genetic predispositions or other environmental factors (Norton et al. 2005; Schellenberg and Lima 2024). Indeed, we have demonstrated that "musical sleepers," individuals without music training who perform similarly in tasks of music perception as trained musicians, can also demonstrate strengthened neural processing and speech-in-noise perception (Mankel and Bidelman 2018). Differences in education format (e.g., solo vs. group), instrument (e.g., drums vs. voice), music style (e.g., classical vs. folk), and timeline of music training (Smayda et al. 2018) could lead to heterogenous differences in sound perception among "musicians" (Tervaniemi 2009), and perhaps result in diverse decision strategies that affect performance (Roark et al. 2022; Smayda et al. 2015). Our own data support different task strategies, showing distinct, learningrelated hemispheric patterns of neural circuitry between groups in a concurrent speech perception task (MacLean et al. 2024).

Another limitation of this study is that we did not examine auditory working memory or attention, cognitive processes which have been associated with music training (Koelsch et al. 1999; Parbery-Clark, Skoe, Lam, and Kraus 2009; Strait et al. 2010; Zuk et al. 2014). Though, we note that cognitive differences among musicians and nonmusicians are not always consistently observed in these abilities (Escobar et al. 2020). Despite these caveats, our data nevertheless demonstrate neural differences in alpha-band oscillatory activity and auditory-motor connectivity between individuals who differ in their amount of self-reported music training, but do not differ with respect to important demographic variables such as age or language experience. Still, future longitudinal studies are needed to confirm interactions between oscillatory activity and music training with regard to concurrent speech perception.

## 5 | Conclusion

We observed stronger alpha-band oscillatory activity preceding incorrect behavioral responses to speech stimuli in musicians. Our findings support the notion that alpha-band (~10 Hz) arousal/suppression in brain activity is an important modulator of trial-by-trial success in perceptual processing, especially for musicians. Musicians' stronger auditory-motor connectivity in the right hemisphere suggests heavier reliance on spectral information with increased music training. Finally, increased bottom-up auditory-motor connectivity for both groups implies greater use of stimulus-specific features rather than temporal expectations during the double-vowel task. Overall, our findings contribute to the understanding of how musicianship may interact with oscillatory mechanisms to shape speech perception.

#### Author Contributions

Jessica MacLean: conceptualization (equal), data curation (lead), formal analysis (lead), investigation (lead), methodology (supporting), project administration (lead), validation (equal), visualization (equal), writing - original draft (lead), writing - review and editing (lead). Jack Stirn: data curation (supporting), investigation (supporting), visualization (supporting), writing - review and editing (supporting). Gavin Bidelman: conceptualization (lead), formal analysis (equal), funding acquisition (lead), investigation (supporting), methodology (supporting), resources (lead), software (equal), supervision (lead), validation (equal), visualization (equal), writing - original draft (supporting), writing - review and editing (supporting).

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#### **Conflicts of Interest**

The authors declare no conflicts of interest.

#### Data Availability Statement

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

#### Peer Review

The peer review history for this article is available at https://www.webof science.com/api/gateway/wos/peer-review/10.1111/ejn.70100.

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