



Plasticity in auditory categorization is supported by differential engagement of the auditory-linguistic network

Gavin M. Bidelman^{a,b,c,*}, Brea Walker^{a,d,e,1}

^a Institute for Intelligent Systems, University of Memphis, Memphis, TN, USA

^b School of Communication Sciences & Disorders, University of Memphis, Memphis, TN, USA

^c University of Tennessee Health Sciences Center, Department of Anatomy and Neurobiology, Memphis, TN, USA

^d Department of Psychology, University of Memphis, Memphis, TN, USA

^e Department of Mathematical Sciences, University of Memphis, Memphis, TN, USA

ARTICLE INFO

Keywords:

Auditory event-related potentials (ERPs)

Categorical perception (CP)

Experience-dependent plasticity

Musical training

Functional brain connectivity

ABSTRACT

To construct our perceptual world, the brain categorizes variable sensory cues into behaviorally-relevant groupings. Categorical representations are apparent within a distributed fronto-temporo-parietal brain network but how this neural circuitry is shaped by experience remains undefined. Here, we asked whether speech and music categories might be formed within different auditory-linguistic brain regions depending on listeners' auditory expertise. We recorded EEG in highly skilled (musicians) vs. less experienced (nonmusicians) perceivers as they rapidly categorized speech and musical sounds. Musicians showed perceptual enhancements across domains, yet source EEG data revealed a double dissociation in the neurobiological mechanisms supporting categorization between groups. Whereas musicians coded categories in primary auditory cortex (PAC), nonmusicians recruited non-auditory regions (e.g., inferior frontal gyrus, IFG) to generate category-level information. Functional connectivity confirmed nonmusicians' increased left IFG involvement reflects stronger routing of signal from PAC directed to IFG, presumably because sensory coding is insufficient to construct categories in less experienced listeners. Our findings establish auditory experience modulates specific engagement and inter-regional communication in the auditory-linguistic network supporting categorical perception. Whereas early canonical PAC representations are sufficient to generate categories in highly trained ears, less experienced perceivers broadcast information downstream to higher-order linguistic brain areas (IFG) to construct abstract sound labels.

1. Introduction

Mapping sensory cues in the environment onto common perceptual identities is a prerequisite for complex auditory processing. In speech perception, acoustically distinct sounds along a continuum of similar features are identified categorically in that they are heard as belonging to one of only a few discrete phonetic classes (Pisoni and Luce, 1987). Because categories represent knowledge of stimulus groupings, patterns, and the linkage of sensory cues with internal memory representations (Seger and Miller, 2010), it is argued that categorization reflects the nexus between perception and cognition (Freedman et al., 2001). Understanding how the brain imposes these “top-down” transformation(s) onto the “bottom-up” sensory input to construct meaningful categories is among the many broad and widespread interests to understand how

sensory features are realized as invariant perceptual objects (Phillips, 2001; Pisoni and Luce, 1987).

The process of categorization requires a higher-order abstraction of the sensory input and consequently, offers an ideal window into how experiential factors might alter this fundamental mode of auditory perception-cognition. Both behavioral and neuroimaging studies demonstrate category-level sensitivity is malleable to listening experience, learning, and stimulus familiarity (Myers, 2014). While categorical perception (CP) emerges early in life (Eimas et al., 1971), it can be further modified by native language experience (Bidelman and Lee, 2015; Kuhl et al., 1992; Xu et al., 2006). Trained musicians also show sharper categorical boundaries than their nonmusician peers for pitch intervals of the musical scale (Burns and Campbell, 1994; Burns and Ward, 1978; Zatorre, 1983). Conceivably, long-term experience and increased

* Corresponding author. School of Communication Sciences & Disorders, University of Memphis, 4055 North Park Loop, Memphis, TN, 38152, USA.

E-mail address: gmbdlman@memphis.edu (G.M. Bidelman).

¹ Currently at the Department of Customer Experience Business Intelligence and Insights, FedEx Services World Headquarters, Memphis, TN, USA.

familiarity with the sounds of a certain domain, whether speech or music, strengthens learned identities in its acoustic space and enhances categorical processing (Bidelman and Lee, 2015; Iverson et al., 2003; Kuhl, 2004; Moon et al., 2013).

Human neurophysiological recordings (M/EEG, fMRI) have revealed a distributed fronto-temporo-parietal neural network supporting auditory categorization including bilateral superior temporal gyrus (STG), inferior parietal, motor cortex, and prefrontal regions (Alho et al., 2016; Bidelman and Lee, 2015; Binder et al., 2004; Chang et al., 2010; Feng et al., 2018; Golestani et al., 2002; Golestani and Zatorre, 2004; Lee et al., 2012; Liebenthal et al., 2010; Luthra et al., 2019; Myers and Blumstein, 2008; Myers et al., 2009). Specific recruitment of these areas is modulated by task demands (Feng et al., 2018), item feedback (Yi and Chandrasekaran, 2016) and attention (Bidelman and Walker, 2017), whether categorization is rule-based or implicit (Yi et al., 2016), stimulus familiarity (e.g., native vs. nonnative speech: Bidelman and Lee, 2015), and presumably, the acoustic domain in which behavior is operating (e.g., speech vs. music). Particularly important to CP is a strong neural interface between temporal and frontal cortices (Bizley and Cohen, 2013; Blumstein et al., 1977; Chevillet et al., 2013; DeWitt and Rauschecker, 2012; Jiang et al., 2018; Luthra et al., 2019). Still, neuroimaging work is equivocal on the locus of categorical (perceptually invariant) brain representations with regard to auditory-linguistic hubs of the CP network. Intracranial recordings suggest abstract speech categories arise within primary auditory cortex (PAC) (Bouton et al., 2018; Chang et al., 2010) whereas fMRI implicates left inferior frontal gyrus (IFG) in categorical formation (Lee et al., 2012; Myers et al., 2009; but see Staeren et al., 2009). A possible reconciliation of divergent findings may be that PAC and IFG are differentially engaged during CP depending on intrinsic and extrinsic influences such as stimulus factors, lexical competition, and listening experience (e.g., Bidelman and Lee, 2015; Bidelman et al., in press; Luthra et al., 2019). Under investigation here is whether PAC-IFG pathways underlying auditory categorical decisions might be shaped and even differentially engaged in an experience-dependent manner. That is, we asked whether categories are formed within *different* auditory-linguistic brain regions in highly skilled vs. less experienced listeners.

To this end, we took a neuroethological approach (Suga, 1989) to investigate the neural mechanisms underlying auditory categorization by examining individuals with highly exaggerated and specialized listening abilities: musicians. Musicians represent an ideal human model to understand experience-dependent plasticity in auditory perceptual-cognitive functions (Alain et al., 2014; Herholz and Zatorre, 2012; Kraus and Chandrasekaran, 2010; Moreno and Bidelman, 2014; Munte et al., 2002; Zatorre and McGill, 2005). Germane to the current study, we recently demonstrated that trained musicians have enhanced (faster and more discrete) categorization of speech sounds compared to their nonmusician peers (Bidelman, 2017; Bidelman and Alain, 2015; Bidelman et al., 2014). These behavioral benefits were accompanied by electrophysiological enhancements in auditory coding 150–200 ms after sound onset. While the underlying locus of these neuroplastic effects (observed in scalp EEG) has yet to be defined, their early latency (<200 ms) strongly implies categorical representations might exist as early as PAC, at least in highly trained listeners (i.e., musicians).

To probe these questions, we recorded high-density neuroelectric brain activity (EEG) in musicians and nonmusicians while they rapidly categorized speech and musical sounds. Source reconstruction and functional connectivity analyses parsed the underlying brain mechanisms of categorization and differential engagement of auditory-linguistic hubs of the CP network depending on experience. Following notions that musicianship expands speech selective brain regions (Dick et al., 2011) and automatizes categorical processing (Bidelman and Alain, 2015; Bidelman et al., 2014; Elmer et al., 2012), we hypothesized early cortical representations in PAC would suffice categorization in highly trained listeners. If PAC representations are weaker (less

categorically organized) in unskilled listeners, we further predicted nonmusicians would require additional recruitment of IFG to enable successful categorization. Domain-specificity was tested by comparing neurobehavioral responses to speech vs. music. We hypothesized musicians would show improved categorization of music given their domain experience and moreover, that these benefits would perhaps be supported by similar neurobiological enhancements as found for speech. Our findings reveal a double dissociation in functional recruitment of the auditory-linguistic network (PAC-IFG) subserving CP that depends on musicianship and stimulus domain. Whereas highly experienced listeners (musicians) show categorical neural organization in early PAC, inexperienced listeners (nonmusicians) must broadcast information to higher-order linguistic brain areas (IFG) to generate category representations.

2. Materials & methods

2.1. Participants

Twenty young adults participated in the experiment: 10 musicians (6 female) and 10 nonmusicians (9 female). All reported normal hearing sensitivity (≤ 25 dB HL; 500–4000 Hz) and no history of neuropsychiatric illness. Musicians (M) were defined as amateur instrumentalists with ≥ 8 years of continuous private instruction on their principal instrument ($mean \pm SD$; 15.0 ± 6.2 yrs), beginning prior to age 12 (6.9 ± 3.2 yrs). Nonmusicians (NM) had <2 years of lifetime music training (0.61 ± 0.85 yrs). These inclusion criteria are consistent with previous reports on musicianship and neuroplasticity (Mankel and Bidelman, 2018; Parbery-Clark et al., 2009; Wong et al., 2007; Yoo and Bidelman, 2019; Zedel and Alain, 2009). All but one participant was right-handed (Oldfield, 1971) and all were native speakers of American English. The two groups were otherwise matched in age (M: 22.4 ± 4.5 yrs, NM: 22.5 ± 2.8 yrs; $t_{18} = -0.06$, $p = 0.95$), years of formal education (M: 16.6 ± 3.3 yrs, NM: 17.1 ± 2.2 yrs; $t_{18} = -0.04$, $p = 0.97$), and gender balance (Fisher exact test, $p = 0.30$). Participants were paid for their time and gave written informed consent in compliance with a protocol approved by the University of Memphis IRB.

2.2. Stimuli

We used speech and music continua from our previous reports on the neural mechanisms of CP (Bidelman and Alain, 2015; Bidelman et al., 2013b, 2014; Bidelman and Walker, 2017).

Speech continuum. Speech tokens comprised a five-step synthetic vowel continuum (Bidelman et al., 2013b) (Fig. 1a). Tokens were 100 ms (10 ms ramps). Each contained an identical voice fundamental (F0), second (F2), and third formant (F3) frequencies (F0: 150, F2: 1090, and F3: 2350 Hz). F1 was parameterized over five equidistant steps (430–730 Hz) resulting in perceptual phonetic continuum from/u/to/a/.

Music continuum. We used a comparable five-step continuum of pitch intervals to assess CP for music (Bidelman and Walker, 2017) (Fig. 1b). Individual notes were synthesized using complex-tones (10 iso-amplitude harmonics; 100 ms duration). For each token, the lower tone of the dyad was fixed with a F0 of 150 Hz (matching the F0 of the speech continuum) while the upper tone's F0 varied over five equal steps to produce a perceptual continuum of musical intervals between the minor (m3; $f_{lower} = 150$, $f_{higher} = 180$ Hz) and major (M3; $f_{lower} = 150$, $f_{higher} = 188$ Hz) third on the chromatic scale (Burns and Ward, 1978). The m3 and M3 intervals connote the valence of "sadness" (m3) and "happiness" (M3) even to non-musicians (Brattico et al., 2009) and are easily described to listeners unfamiliar with music-theoretic labels (Bidelman and Walker, 2017). Before the start of the task, listeners were allowed to replay the continuum's endpoints as practice trials to familiarize themselves with the music labels.

2.3. Task procedure

During EEG recording, listeners heard 200 randomly ordered exemplars of each speech/music token (each domain presented in separate blocks). They were asked to label each sound with a binary response as quickly and accurately as possible (*speech*: “u” or “a”; *music*: “minor 3rd” or “major third”). Stimuli were delivered binaurally at 83 dB SPL through insert earphones (ER-2; Etymotic Research). The interstimulus interval (ISI) was jittered randomly between 400 and 600 ms (20 ms steps, rectangular distribution) following listeners’ behavioral response to avoid anticipating the next trial and rhythmic entrainment of the EEG.

2.4. EEG recording and preprocessing

Continuous EEGs were recorded from 64 sintered Ag/AgCl electrodes at standard 10-10 locations around the scalp (Oostenveld and Praamstra, 2001). Recordings were sampled at 500 Hz (SynAmps RT amplifiers; Compumedics Neuroscan) and passband filtered online (DC-200 Hz). Electrodes placed on the outer canthi of the eyes and the superior and inferior orbit were used to monitor ocular movements. During acquisition, electrodes were referenced to an additional sensor placed ~1 cm posterior to the Cz channel. Data were re-referenced off-line to the common average for analysis (Bertrand et al., 1985). Contact impedances were maintained <10 kΩ during data collection.

Subsequent preprocessing was performed in Curry 7 (Compumedics Neuroscan) and BESA[®] Research (v7) (BESA, GmbH). Ocular artifacts (i.e., blinks and saccades) were first corrected in the continuous EEG using a principal component analysis (PCA) (Picton et al., 2000). Cleaned EEGs were then digitally filtered (1–30 Hz; zero-phase filters), epoched (-200-800 ms), baseline corrected to the prestimulus interval, and ensemble averaged to derive responses for each stimulus condition per participant. This resulted in 10 ERP waveforms per participant (5 tokens x 2 stimulus domains).

2.5. Behavioral data analysis

For each continuum, identification scores were fit with a two-parameter sigmoid function: $P = 1/[1 + e^{-\beta_1(x-\beta_0)}]$, where P is the proportion of trials identified as a given vowel, x is the step number along the stimulus continuum, and β_0 and β_1 the location and slope of the logistic fit estimated using nonlinear least-squares regression (Bidelman and Walker, 2017; Bidelman et al., 2014). These parameters were used to assess differences in the location and “steepness” (i.e., rate of change) of

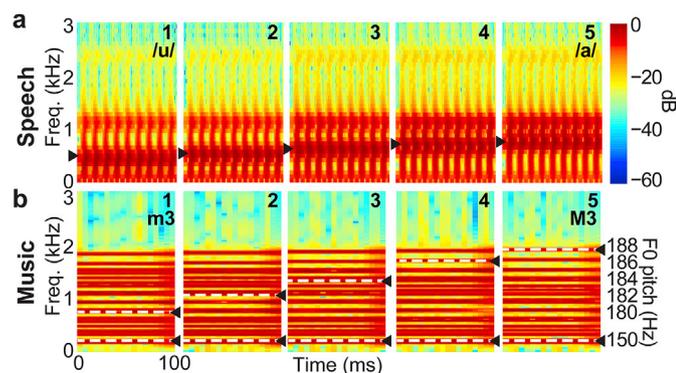


Fig. 1. Spectrograms of speech and music continua used to probe experience-dependent plasticity in CP. (a) For speech, vowel first formant frequency was varied across five equal steps (430–730 Hz; ►) creating a continuum from /u/ to /a/. (b) For music, tone complexes formed two-tone pitch intervals (white dotted lines) spanning a continuum from a minor (m3) to major (M3) third. Stimuli were otherwise matched in duration (100 ms), intensity (83 dB SPL), and starting pitch height ($F_0 = 150$ Hz). Reproduced from Bidelman and Walker (2017) with permission from Jon Wiley and Sons.

the categorical boundary as a function of stimulus domain (i.e., speech vs. music) and group (M vs. NM). Larger β_1 values reflect steeper psychometric functions and hence, indicate stronger CP. Behavioral speech labeling speeds (i.e., reaction times; RTs) were computed as listeners’ median response latency across trials for a given condition. RTs outside 250–2500 ms were deemed outliers and excluded from further analysis (Bidelman et al., 2013b; Bidelman and Walker, 2017).

2.6. Electrophysiological data analysis

Source reconstruction. Neuronal sources of evoked potentials must be inferred given the volume-conducted nature of the scalp-recorded EEG and “cross-talk” between adjacent sensor measurements. To more directly assess the neural generators underlying experience-dependent plasticity in CP, we transformed sensor (electrode)-level recordings to source space using discrete inverse models. We used Classical Low Resolution Electromagnetic Tomography Analysis Recursively Applied (CLARA) [BESA (v7)] (Iordanov et al., 2014) to estimate the neuronal current density underlying the scalp potentials for speech (e.g., Alain et al., 2017; Bidelman et al., 2018). CLARA models the inverse solution as a large collection of elementary dipoles distributed over nodes on a mesh of the cortical volume. The algorithm estimates the total variance of the scalp-recorded data and applies a smoothness constraint to ensure current changes minimally between adjacent brain regions (Michel et al., 2004; Picton et al., 1999). CLARA renders more focal source images by iteratively reducing the source space during repeated estimations. On each iteration (x3), a spatially smoothed LORETA solution (Pascual-Marqui et al., 2002) was recomputed and voxels below a 1% max amplitude threshold were removed. This provided a spatial weighting term for each voxel on the subsequent step. Three iterations were used with a voxel size of 7 mm in Talairach space and regularization (parameter accounting for noise) set at 0.01% singular value decomposition. Group-level statistical (t -stat) maps were computed using the ‘ft_sourcestatistics’ function in the MATLAB FieldTrip toolbox (Oostenveld et al., 2011) and threshold at $\alpha = 0.05$. Source activations were then visualized by projecting them onto the semi-inflated MNI adult brain template (Fonov et al., 2009).

From each CLARA volume (i.e., activation timecourse per voxel), we extracted the amplitude of source activity in predefined regions of interest (ROIs) including bilateral primary auditory cortex (PAC) and inferior frontal gyrus (IFG) near Broca’s area (see Fig. 4). These ROIs were selected given their known role in complex speech perception including auditory categorization (e.g., Alain et al., 2018; Bidelman et al., 2018; Bidelman and Howell, 2016; Bizley and Cohen, 2013; Du et al., 2014; Mazziotta et al., 1995; Scott and Johnsrude, 2003). The spatial resolution of CLARA is 5–10 mm (Iordanov et al., 2014, 2016), which is considerably smaller than the distance between PAC and IFG (~40 mm; Mazziotta et al., 1995).

To quantify the degree to which neural responses showed categorical coding, we averaged source amplitudes to prototypical tokens at the ends of the continua and compared this combination to the ambiguous token at their midpoint (e.g., Bidelman, 2015; Bidelman and Walker, 2017; Liebenthal et al., 2010). This contrast (mean[Tk1, Tk5] vs. Tk3) allowed us to assess the degree to which each groups’ neural activity differentiated stimuli with well-formed categories from those heard with a bistable (ambiguous) identity within the speech and music domains.

To quantify brain-behavior relationships, we extracted overall response amplitude within the PAC and IFG ROI centroids, computed at the latency of maximum global field power (GFP) on the scalp (Lehmann and Skrandies, 1980) (see Fig. 4a). We localized responses using peak GFP which represents a single, reference free measure of response strength at the head surface (Murray et al., 2008). This data driven approach is less biased than localizing individual *a priori* selected ERP waves—which change considerably over the topography of the scalp (Murray et al., 2008). Peak GFP occurred at 288 ms for speech and 226 ms for music. We used Spearman correlations to assess if PAC vs. IFG

amplitudes predicted the slopes of listeners' psychometric functions when categorizing stimuli per domain (speech, music). This analysis was repeated for both left and right hemispheres to test whether lateralized activity was more predictive of behavior in a certain domain (e.g., right PAC driving music CP; left PAC driving speech CP).

Functional connectivity. We measured causal (directed) flow of information within the auditory-linguistic brain network using Granger Causality (GC) (Geweke, 1982; Granger, 1969). This analysis was restricted to only the PAC and IFG ROIs to test our specific hypothesis regarding plasticity in the auditory-linguistic circuit (see Introduction). Functional connectivity was computed in BESA Connectivity (v1), which computes GC in the frequency domain (Geweke, 1982) using non-parametric spectral factorization on single-trial time-frequency maps (Dhamala et al., 2008). The frequency decomposition was based on complex demodulation (Papp and Ktonas, 1977), akin to a short-term (running) Fourier transform, that provides uniform frequency resolution across the bandwidth of analysis. Signal X is said to "Granger-cause" signal Y if past values of X contain information that predict Y above and beyond information contained in past values Y alone. Importantly, GC can be computed directionally (e.g., $X \rightarrow Y$ vs. $Y \rightarrow X$) to infer causal flow between interacting brain signals. We computed GC between PAC and IFG activity using full-band (1–30 Hz) responses at the latency corresponding to the max GFP (see Fig. 4a), where neural responses showed group differences in the CLARA maps. Connectivity was computed in both the afferent (PAC \rightarrow IFG) and efferent (IFG \rightarrow PAC) directions to assess "bottom-up" vs. "top-down" neural signaling (Bidelman et al., 2018). Connectivity was only computed for the Tk1/5 tokens to avoid neural signaling that might be related to resolving ambiguous (bistable) sounds (Tk 3) and because these tokens elicited stronger responses than the midpoint tokens (i.e., Tk1/5 > Tk3; Fig. 4b).

3. Results

3.1. Behavioral categorization (% , RTs)

Fig. 2 shows behavioral psychometric identification functions for Ms and NMs when classifying speech (Fig. 2a) and music (Fig. 2b). Listeners' identification was generally dichotomous as indicated by an abrupt shift in perception midway through the continua. For NMs, music stimuli elicited more continuous perception as indicated by the lack of any abrupt perceptual shift and linear/flat psychometric function. Both Ms and NMs showed stronger CP for speech than music [M : $t_{18} = 2.38$, $p = 0.028$; NM : $t_{18} = 6.36$, $p < 0.0001$]. However, Ms demonstrated considerably sharper perceptual boundaries than NMs for both speech [β_1 parameter; $t_{18} = 2.23$, $p = 0.034$] and music [$t_{18} = 2.85$, $p = 0.011$] continua. These findings suggest that while CP is stronger for speech than musical sounds, musicians show enhanced perceptual categorization in both auditory domains.

Behavioral RTs for speech and music categorization are shown for each group in Fig. 2c and d. An ANOVA conducted on speech labeling speeds revealed RTs were modulated across vowel token [$F_{4, 72} = 32.60$, $p < 0.0001$]. There was no effect of group [$F_{1, 18} = 1.17$, $p = 0.29$] which might be expected given the overlearned nature of vowels for our native English speakers. Still, both Ms [$t_{72} = 9.12$, $p < 0.0001$] and NMs [$t_{72} = 6.11$, $p < 0.0001$] showed the characteristic slowing near the CP boundary (token 3) relative to other tokens along the continuum [i.e., $\text{mean}(\text{Tk}1,2,4,5) < \text{Tk}3$], consistent with previous reports examining speeded speech classification (Bidelman et al., 2013b; Bidelman and Walker, 2017; Pisoni and Tash, 1974). For music, we found a group x token interaction [$F_{4, 72} = 2.59$, $p = 0.043$]. Interestingly, Ms showed a categorical slowing in RTs near the ambiguous midpoint [$t_{72} = 2.05$, $p = 0.044$] but this bowing effect was not observed in NMs [$t_{72} = -1.33$, $p = 0.19$]. This again suggests music was perceived less categorically in NMs compared to trained Ms.

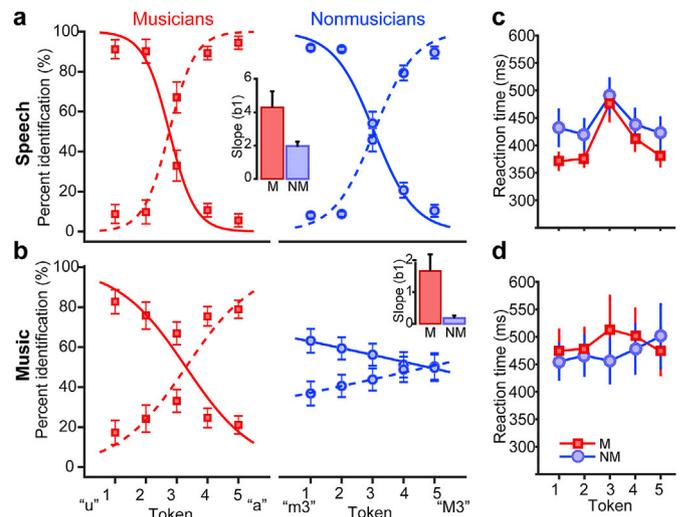


Fig. 2. Perceptual categorization for speech and music is enhanced in musicians. (a) Psychometric identification functions for speech show an abrupt shift in behavior indicative of discrete CP. (b) Music identification is discrete (categorical) in Ms but continuous in NMs. Ms show stronger CP than NMs (steeper identification curves) in both domains (insets). (c-d) Reaction times for classifying stimuli. Listeners are slower to label speech near the categorical boundary (Tk 3), indicative of CP (Bidelman et al., 2013b; Pisoni and Tash, 1974) but Ms are faster at making categorical judgments across the board. Ms show a similar categorical speed effect (bowing in RTs) for music that is not observed in NMs. errorbars = ± 1 s.e.m.; M, musicians; NM, nonmusicians.

3.2. Electrophysiological data

Butterfly ERP plots (sensor-level potentials) are shown per group and stimulus domain in Fig. 3. Visual inspection of the data revealed more robust cortical responses in Ms compared to NMs for both speech and musical sounds, particularly at fronto-central electrodes where CP effects appear most prominent on the scalp surface (e.g., Bidelman and Walker, 2017; Liebenthal et al., 2010). A two-way, mixed-model ANOVA (group x stimulus token; subject = random) revealed ERP N1–P2 magnitudes at the vertex (Cz electrode, Fig. 3) were stronger in musicians to music across the board ($F_{1, 18} = 6.10$, $p = 0.0217$). Similarly, Ms' responses were stronger for speech but with a group x token interaction ($F_{4, 72} = 3.69$, $p = 0.0086$), whereby group differences emerged primarily for vowels 1 and 2. These scalp data replicate a growing number of studies reporting larger auditory ERP responses in trained musicians (Baumann et al., 2008; Bidelman and Alain, 2015; Bidelman et al., 2014; Musacchia et al., 2008; Reinke et al., 2003; Seppänen et al., 2012; Shahin et al., 2003). However, the volume-conducted nature of sensor-space (i.e., electrode) recordings did not allow us to separate the underlying sources that contribute to these group effects. Consequently, we focused our subsequent analyses in source space to directly assess the neural generator characteristics underlying plasticity in auditory categorical processing.

CLARA imaging parsed the underlying neural mechanisms responsible for Ms' enhanced CP and these electrode-level effects (Fig. 4). Pooling across tokens within each continuum, neural activity peaked ~ 50 ms later for speech than music (GFP_{speech} latency: 288 ms; GFP_{music} latency: 226 ms; Fig. 4a). To quantify the degree of categorical neural coding, we averaged source amplitudes to prototypical tokens at the end of the continua and compared this combination to the ambiguous midpoint token (e.g., Bidelman, 2015; Bidelman and Walker, 2017; Liebenthal et al., 2010). This contrast allowed us to assess when and where neural responses (CLARA maps) differentiated stimuli with well-formed categories from those heard with a bistable (ambiguous)

identity. Contrasts of this categorical coding effect revealed a double-dissociation within auditory-linguistic brain regions depending on group and stimulus domain (Fig. 4 b,c). For speech, musicians showed stronger categorical responses in PAC bilaterally, whereas in non-musicians, categorical speech responses were observed primarily in left IFG. For music, Ms showed stronger categorical responses than NMs in right PAC. In contrast, categorical coding for music was stronger in NMs in left precentral gyrus (motor cortex), a region previously identified to predict CP for speech (Chevillet et al., 2013). These results suggest a differential engagement of the auditory-linguistic-motor loop during auditory categorization depending on musicianship.

Brain-behavior correlations again revealed a double-dissociation in the predictive power of PAC vs. IFG in predicting behavior. Across cohorts, larger categorical speech activity ($Tk1/5 > Tk3$) in left PAC (as in Ms) was associated with more dichotomous CP (steeper psychometric slopes) [$r = 0.46, p = 0.042$] (Fig. 5b). We found the reverse in left IFG which negatively correlated with behavior [$r = -0.68, p = 0.0009$] (Fig. 5a), where stronger neural activity predicted poorer perception. Neither right hemisphere ROI nor any of the music responses correlated with behavior (all $ps > 0.27$; data not shown).

Increased involvement of IFG in nonmusicians could reflect the need to recruit additional higher-order (linguistic) brain areas downstream if neural representations in auditory cortex are insufficient for categorization. We tested this possibility by measuring directed functional connectivity between PAC and IFG using Granger causality (GC), an information-theoretic measure of causal signal interactions (Geweke, 1982; Granger, 1969). GC values were cube-root transformed to improve homogeneity of variance assumptions for parametric statistics and to account for the lower bound of GC values ($=0$). A three-way, mixed-model ANOVA (group \times stimulus domain \times hemisphere; subject = random) revealed a significant group \times stimulus interaction [$F_{1, 36} = 6.89, p = 0.0126$] on afferent connectivity, meaning the strength of PAC \rightarrow IFG signaling was modulated dependent on listeners' musical training and whether they were categorizing speech or music. By hemisphere, we found a stimulus \times group effect in LH [$F_{1, 36} = 4.76, p = 0.0358$] (Fig. 6a). Tukey-Kramer comparisons revealed the LH interaction was attributable to stronger feedforward connectivity for speech than music in NMs (i.e., speech $>$ music; $p = 0.0495$), whereas musicians' LH PAC \rightarrow IFG connectivity was equally strong between stimulus domains (i.e., speech = music; $p = 0.25$). By domain, contrasts showed marginally stronger PAC \rightarrow IFG connectivity in NMs vs. Ms for speech ($p = 0.08$) but not music ($p = 0.21$). In contrast, no effects in RH

afferent connectivity were significant (all $ps > 0.122$) (Fig. 6b).

No significant effects were found for LH efferent connectivity (IFG \rightarrow PAC) (data not shown; all $ps > 0.45$). The stimulus \times group effect in RH IFG \rightarrow PAC was marginal ($F_{1, 36} = 4.20, p = 0.048$), but none of the pairwise contrasts survived multiple corrections. Thus, there was insufficient evidence to suggest stimulus or group differences in top-down signaling. However, afferent signaling was stronger than efferent signaling overall [i.e., (PAC \rightarrow IFG) $>$ (IFG \rightarrow PAC); $F_{1, 108} = 6.30, p = 0.0135$]. These connectivity findings confirm a differential engagement of left-lateralized auditory-linguistic network (specifically in the PAC \rightarrow IFG direction) between musicians and nonmusicians during auditory categorization that also depends on stimulus domain.

4. Discussion

By measuring electrical brain activity in highly specialized (musician) vs. less experienced (nonmusician) listeners we demonstrate that categorical processing for speech and musical sounds varies in an experience-dependent manner. Our EEG data reveal the mechanisms underlying these behavioral enhancements are accompanied by different engagement and neural signaling within the auditory-linguistic pathway (PAC-IFG) that critically depend on listening experience. Whereas highly skilled musicians code auditory categories in primary auditory cortex (PAC), nonmusicians show additional recruitment of non-auditory regions (e.g., inferior frontal gyrus, IFG) to successfully generate category-level information. Our findings provide new evidence that the brain arrives at categorical labels through different operational "modes" within an identical PAC-IFG pathway. Whereas early canonical PAC representations are sufficient to generate categories in highly trained ears, less experienced listeners must broadcast information downstream to non-canonical, higher-order linguistic brain areas (IFG) to construct abstract sound labels.

Our data confirm enhanced categorization of musical sounds in musicians (Burns and Ward, 1978; Howard et al., 1992; Klein and Zatorre, 2011; Locke and Kellar, 1973; Siegel and Siegel, 1977; Zatorre and Halpern, 1979). This supports notions that music expertise warps or restricts the perceptual space near category boundaries, sharpening the internal representations of auditory categories and supplying more behaviorally-relevant decisions when classifying sound objects (Bidelman and Alain, 2015; Bidelman et al., 2014). Nonmusicians' weaker CP for music can be parsimoniously explained as an unfamiliarity in associating verbal labels to the pitch intervals of music. Just as language

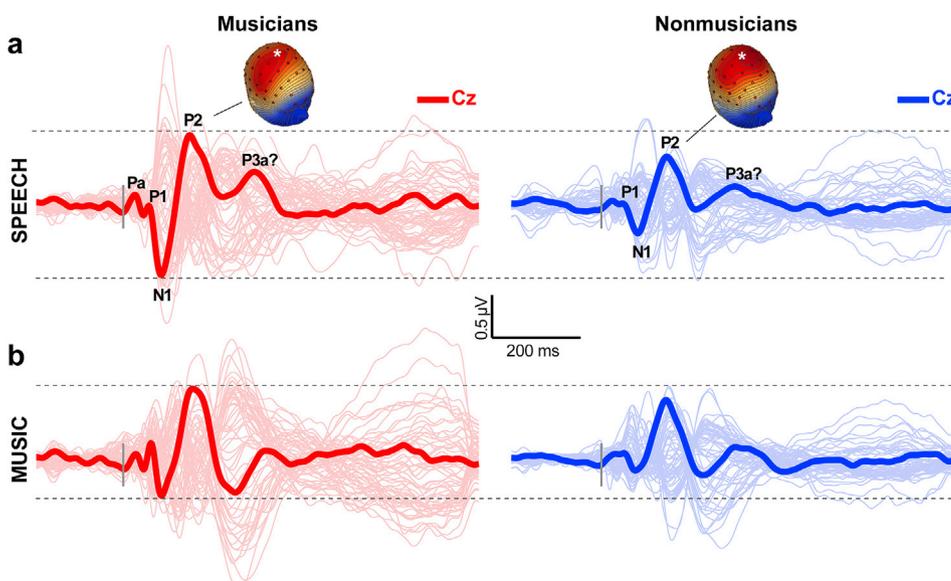


Fig. 3. Scalp-recorded event-related brain potentials (ERPs) show stronger neural responses to speech and music in musicians. Grand averaged butterfly plot of neuroelectric time waveforms per group and stimulus domain. Cortical ERPs appear as biphasic deflections (e.g., P1–N1–P2 “waves”) within ~ 200 ms after the time-locking stimulus. Cz electrode = bold trace. Neural activity is modulated by group and stimulus domain. Scalp topographies are plotted at the latency of the P2 wave (*Cz electrode). Vertical bars = stimulus onset ($t = 0$). Dotted lines, visual aid for group comparisons.

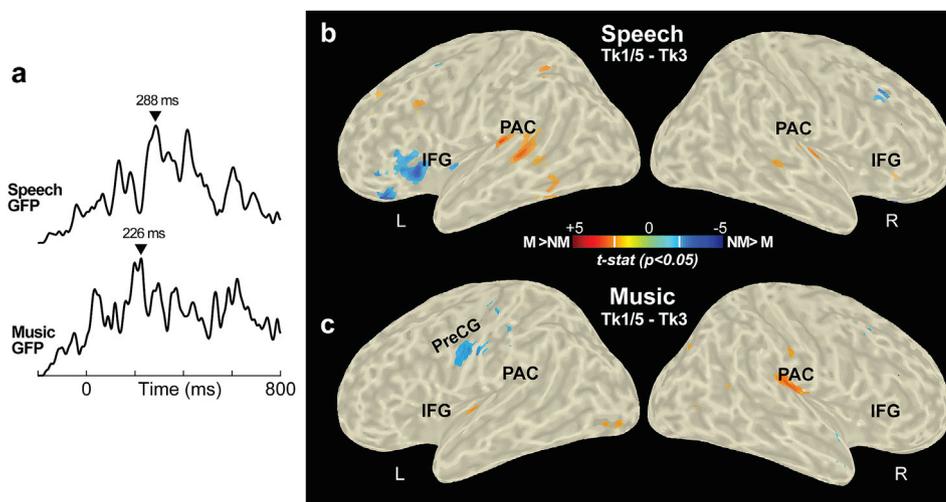


Fig. 4. Source responses reveal differential activation of auditory and linguistic cortex during categorization depending on musical training. (a) Grand average global field power (Lehmann and Skrandies, 1980) (collapsed across tokens and groups) shows the time-course of aggregate neural activity across the scalp for each domain. (b-c) Statistical contrast maps of CLARA activations between musicians and nonmusicians. Maps are shown at the maximum GFP latency (\blacktriangledown , Fig. 4a), projected onto the semi-inflated MNI adult brain template (Fonov et al., 2009) and contrast group differences (t -stat, $p < 0.05$ masked, uncorrected) in the degree of categorical coding (i.e., Tk1/5 – Tk3 effect; Bidelman and Walker, 2017) across the entire brain volume. (b) For speech, categorical coding is observed in bilateral PAC for Ms but left IFG for NMs. (c) For music, Ms show stronger categorical responses than NMs in right PAC; NMs show stronger categorization in left preCG (motor cortex). PAC, primary auditory cortex; IFG; inferior frontal gyrus; preCG, precentral gyrus (primary motor cortex); L/R, left/right hemisphere.

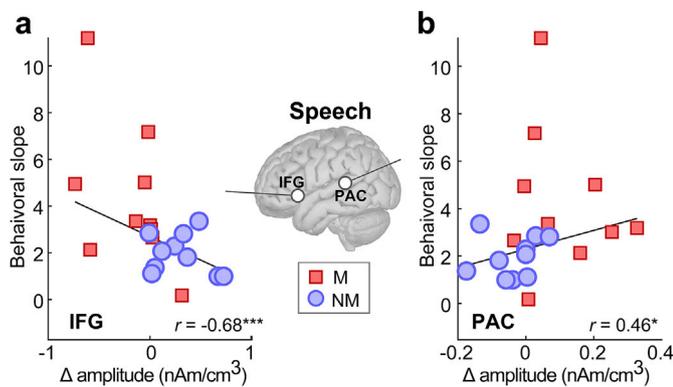


Fig. 5. Brain-behavior correlations reveal a double-dissociation in how PAC and IFG predict behavioral CP in expert and non-expert listeners. Neural responses reflect activations to speech within PAC and IFG at the centroid of each ROI shown (see Fig. 4). MNI coordinates (x,y,z): PAC_{LH} = [-38.5, -37.5, 5.5], PAC_{RH} = [41.5, -26.5, 0.5], IFG_{LH} = [-22.5, 24.5, -2.5], and IFG_{RH} = [23.5, 26.5, -2.5] mm. Larger differentiation of speech (i.e. Δ amplitude: Tk1/5 > Tk3) in left PAC is associated with stronger categorical percepts (steeper psychometric slopes). The reverse is observed in left IFG, where stronger activity predicts poorer behavior. Neither right hemisphere PAC/IFG nor music responses correlated with behavior (data not shown). $*p < 0.05$, $***p < 0.001$.

experience sharpens categories for a speaker's native speech sounds (Bidelman and Lee, 2015; Bradlow et al., 1997; Kuhl et al., 1992; Xu et al., 2006), we find musicians (but not NMs) perceive music categorically. Our findings bolster notions that less familiar sounds not encountered in one's regular experience fail to perceptually organize in a robust categorical manner (e.g., Bidelman and Lee, 2015; Bidelman et al., in press; Bidelman and Walker, 2017; Burns and Campbell, 1994; Burns and Ward, 1978; Xu et al., 2006; Zatorre, 1983) and reveal a strong role of experience in shaping categorical skills.

We also extend prior studies by demonstrating that auditory expertise enhances perceptual categorization of speech (Bidelman and Alain, 2015; Bidelman et al., 2014; Elmer et al., 2012). Musicians' stronger CP in both stimulus domains suggests that intensive listening experience can transfer to benefit CP even in non-musical situations (see also Bidelman et al., 2011a; Chandrasekaran et al., 2009; Hutka et al., 2015; Marie et al., 2011). Unlike for music stimuli, it is difficult to argue for a familiarity

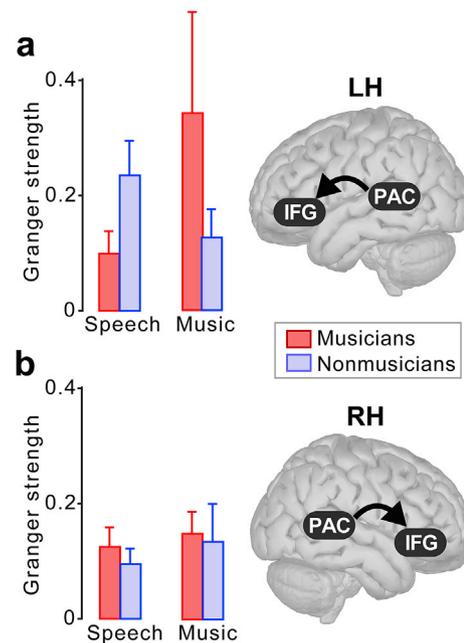


Fig. 6. Functional connectivity reveals experience-dependent changes in causal neural signaling within the auditory-linguistic pathway. (a) Granger causality between PAC directed toward IFG shows stronger communication during speech compared to music categorization in NMs. Contrastively, left PAC→IFG connectivity is invariant across stimulus domains in Ms. (b) PAC→IFG connectivity does not vary in RH. These results suggest a differential engagement of the left-lateralized auditory-linguistic network (PAC→IFG) depending on music expertise. Whereas neural representations in PAC are sufficient for categorization in Ms (see Fig. 4), NMs recruit additional linguistic areas downstream to aid perception. Efferent connectivity (IFG→PAC) did not vary with stimulus domain nor group (data not shown). errorbars = ± 1 s.e.m.

effect in our speech data as musicians were native English speakers. Consequently, we attribute Ms' enhanced CP across domains to reflect both increased familiarity with certain sound labels (especially music) and their higher sensitivity to fine-grained acoustic details, thus enabling superior categorization even for overlearned sounds like speech. As discussed below, musicians' enhanced categorization could stem from musical training automatizing CP to earlier stages of processing (as we

find for PAC, Fig. 4), which would strengthen auditory categories in a relatively domain general manner. The fact we do not find group connectivity differences in the reverse direction (IFG→PAC) argues musicians' benefits in CP are probably not due to general differences in "top-down" control or other attentional mechanisms *per se*, but relate to an enhanced quality of speech representations early in the system (see also Baumann et al., 2008; Bidelman et al., 2014).

EEG data corroborate our behavioral findings by unmasking the underlying brain mechanisms driving experience-dependent changes in auditory categorization. We found musicians had stronger neural encoding of speech and music stimuli across the board (Fig. 3), consistent with previous neuroimaging studies (Bidelman and Alain, 2015; Bidelman et al., 2014; Musacchia et al., 2008; Schneider et al., 2002; Shahin et al., 2003; Wong et al., 2007). These results support growing evidence that musicians' brain responses carry more information relevant to perception than their non-musician counterparts (Bidelman et al., 2014; Elmer et al., 2012; Weiss and Bidelman, 2015). However, we found stark differences in the underlying brain regions mediating each group's CP. Whereas skilled listeners (musicians) were able to code auditory categories in PAC, naïve ears (nonmusicians) showed categorical responses in non-canonical areas including IFG. This double-dissociation in source contribution between groups suggests that listening experience differentially shapes the functional coupling within the auditory-linguistic network.

There is evidence that sound representations in PAC might self-organize due to non-uniformities in cell firing between exemplar vs. non-exemplar sounds (e.g., within vs. between category tokens) (Guenther and Gjaja, 1996). Receptive fields of auditory cortical neurons also show marked changes in their temporal discharge patterns across categorically perceived speech continua (Steinschneider et al., 1999, 2003). Therefore, one interpretation of our data is that musical training enhances CP by automatizing the categorization process and relegating category-level representations to the earliest stages of auditory cortical processing in PAC. On the contrary, PAC representations are insufficient for categorical organization in nonmusicians, and less skilled listeners must compute categories in higher-order IFG downstream. Higher fidelity auditory neural representations local to PAC would tend to speed behavioral decisions and result in steeper, more discrete identification (Bidelman et al., 2019; Bidelman et al., 2019; Rozsypal et al., 1985) as we find in our musician cohort. Alternatively, focal readout of sensory information by prefrontal regions (IFG) (Binder et al., 2004; Bouton et al., 2018) may underlie the increased decision variability we find in nonmusicians.

Consistent with our findings, phoneme category selectivity is observed early (<150 ms) in both PAC and left inferior frontal gyrus (pars opercularis) (Alho et al., 2016; Bidelman et al., 2013b; Chang et al., 2010; Toscano et al., 2018). Cue- and category-based representations are probably not mutually exclusive and may overlap in both time and space within the brain; IFG, for instance, may code acoustic details of speech nearly simultaneously (within ~50 ms) of coding phonological categories (Toscano et al., 2018). Similar phoneme-category selectivity has also been observed in left PreCG and connectivity between posterior aspects of auditory cortex and PreCG mediates complex speech identification decisions (Chevillet et al., 2013). Nonmusicians did show categorical responsivity in PreCG, but only for music. PreCG activation in nonmusicians could reflect increased difficulty of classifying unfamiliar music tokens, which would be expected to evoke non-auditory regions to aid perception (Du et al., 2014). However, our data do not readily support interpretations that sensorimotor interplay within the dorsal auditory-motor stream is sufficient to account for performance in categorization tasks (cf. Chevillet et al., 2013). Rather, we find engagement of non-canonical areas outside the auditory system depends critically on listeners' domain of expertise and therefore what pathways are available and tuned for processing.

Our data align with general notions that non-canonical auditory regions including IFG (Broca's area) and adjacent prefrontal areas play a

major role in categorical processing of speech (Bouton et al., 2018; Lee et al., 2012; Luthra et al., 2019; Meyers et al., 2008; Myers et al., 2009). However, our findings suggest IFG may not play a *domain-general* role in computing category representations (Myers et al., 2009). We found IFG activity anti-correlated with behavior (Fig. 5). Increased IFG activity, as in nonmusicians, was indicative of poorer speech categorization whereas stronger PAC responses predicted better behavioral performance. Thus, while IFG has been implicated in speech identification and categorization (Du et al., 2014; Lee et al., 2012; Luthra et al., 2019), nonmusicians' increased frontal activation could instead be related to increased attentional load (Bouton et al., 2018; Giraud et al., 2004), lexical uncertainty (Luthra et al., 2019), and/or unconscious sensory repair that applies prior knowledge to a noisy input (Shahin et al., 2009). Indeed, decision loads IFG during effortful speech listening (Binder et al., 2004; Bouton et al., 2018; Du et al., 2014) and left IFG is more active when items are perceptually confusable (Feng et al., 2018). Inasmuch as nonmusicians are less skilled listeners and were more challenged by even our simple auditory CP tasks (as suggested by their increased RTs), IFG might necessarily be recruited in a top-down manner to aid categorical predictions on the sensory input.

Supporting this interpretation, studies on categorical speech learning have shown frontal speech regions are relatively less active in "good learners" (Golestani and Zatorre, 2004), mirroring our findings in musicians. IFG may also reflect subvocal rehearsal strategies or articulatory codes that aid speech perception (Du et al., 2014; Golestani and Zatorre, 2004; Hickok and Poeppel, 2004; Papoutsis et al., 2009). Functional coupling between auditory and frontal brain regions is modulated by musical training (current study; Du and Zatorre, 2017) so it stands to reason that nonmusicians' increased involvement of IFG may reflect augmented generation or retrieval of articulatory codes to improve speech categorization. Similarly, the lack of IFG involvement for music may reflect total absence of verbal labels of articulatory code for non-speech stimuli and/or NMs' substantial difficulty in the music task (Fig. 2).

Our data further align with predictive coding models of speech processing (Bouton et al., 2018; Di Liberto et al., 2018). Under this premise, more ambiguous acoustic information might invoke the need to pass information to higher-order frontal areas (IFG) to help interpret weaker sensory representations in PAC in a predictive framework. Our functional connectivity analysis supports this notion (at least for speech) as evidenced by nonmusicians' stronger PAC→IFG neural signaling in left hemisphere. These results indicate that auditory expertise shapes not only regional engagement but also functional interplay (directed communication) between PAC and IFG when making sound-to-label associations (Bizley and Cohen, 2013; Luthra et al., 2019). Our data also corroborate previous studies suggesting music training enhances synchronization between auditory cortices (Kuhnis et al., 2014) and increases global network efficiency between auditory and frontal regions (Du and Zatorre, 2017; Paraskevopoulos et al., 2017).

Our speech and music stimuli were relatively similar complex sounds and we intentionally used common pitch intervals in Western music. Thus, it remains to be seen if musicians' enhanced CP for music extends to non-Western musical systems or other nonspeech sounds. Supporting these possibilities, previous studies have revealed musicians' have enhanced neural differentiation of non-native speech sounds (Bidelman et al., 2011a; Chandrasekaran et al., 2009; Marie et al., 2011) and improved discrimination of micro-tonal pitch patterns (Bidelman et al., 2011b, 2013a). Such increased differential sensitivity may translate to improved verbal category labelling as observed here. Still, an interesting avenue for future work could explore whether musicians' benefits in verbal sound labeling extend to nonverbal discrimination tasks requiring categorical judgments.

Collectively, our findings reveal a dissociation in the networks underlying sound categorization for expert vs. naïve listeners. More broadly, our study provides direct neurobiological evidence that musicianship automatizes critical and fundamental skills that support the

auditory perceptual organization and categorization of sound. From a translational perspective, it is worth noting that some developmental learning disorders including dyslexia have been linked to poorer categorization skills (Calcutt et al., 2016; Hakvoort et al., 2016; Mes-saoud-Galusi et al., 2011; Noordenbos and Serniclaes, 2015; Zoubrinetzky et al., 2016). Yet, recent longitudinal (6 mo) music training studies have shown improvements in categorical processing in dyslexic children in the form of stronger pre-attentive differentiation of speech at post-test (Frey et al., 2019). Such longitudinal interventions are consistent with our cross-sectional observations (present study; Bidelman and Alain, 2015; Bidelman et al., 2014), and imply active music training might fortify complex auditory processing and in turn, enhance the encoding and decoding of sound-to-meaning relations. Conceivably, monitoring changes in the signal routing (connectivity) within the brain, as examined here, could offer future studies new ways to track the success of training programs or identify neural marker(s) of auditory expertise (Mankel and Bidelman, 2018; Strait and Kraus, 2014), which has been a difficult trait to objectively quantify.

Author contributions

G.M.B. designed the experiment, B.W. collected the data, G.M.B. and B.W. analyzed the data and wrote the paper.

Acknowledgements

Requests for data and materials should be directed to G.M.B [gmbdlman@memphis.edu]. This work was supported by the GRAMMY Foundation® and the National Institutes of Health (NIH/NIDCD R01DC016267) awarded to G.M.B.

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