Title: Myogenic artifacts masquerade as neuroplasticity in the auditory frequency-following response (FFR)

Author(s): Gavin M. **Bidelman**[1,2,3,*], Alexandria **Sisson**[1], Rose **Rizzi**[1,2,] Jessica **MacLean**[1,2], and Kaitlin **Baer**[4,5]

Affiliations:

[1]Department of Speech, Language and Hearing Sciences, Indiana University, Bloomington, IN, USA

[2]Program in Neuroscience, Indiana University, Bloomington, IN, USA

[3]Cognitive Science Program, Indiana University, Bloomington, IN, USA

[4]School of Communication Sciences & Disorders, University of Memphis, Memphis, TN, USA

[5]VA Medical Center, Memphis, TN, USA

Author contributions: GMB designed the experiment, AS, RR, JM, and KB collected the data, GMB analyzed the data, and GMB, AS, RR, JM, and KB wrote the paper.

Competing interests: The authors declare no competing interests.

***Address for editorial correspondence:**
Gavin M. Bidelman, PhD
Department of Speech, Language and Hearing Sciences
Indiana University
2631 East Discovery Parkway
Bloomington IN, 47408
TEL: (812) 855-9339
Email: gbidel@indiana.edu

Abstract

The frequency-following response (FFR) is an evoked potential that provides a “neural fingerprint” of complex sound encoding in the brain. FFRs have been widely used to characterize speech and music processing, experience-dependent neuroplasticity (e.g., learning, musicianship), and biomarkers for hearing and language-based disorders that distort receptive communication abilities. It is widely assumed FFRs stem from a mixture of phase-locked neurogenic activity from brainstem and cortical structures along the hearing neuraxis. Here, we challenge this prevailing view by demonstrating upwards of ~50% of the FFR can originate from a non-neural source: contamination from the postauricular muscle (PAM) vestigial startle reflex. We first establish PAM artifact is present in all ears, varies with electrode proximity to the muscle, and can be experimentally manipulated by directing listeners’ eye gaze toward the ear of sound stimulation. We then show this muscular noise easily confounds auditory FFRs, spuriously amplifying responses by 3-4x fold with tandem PAM contraction and even explaining putative FFR enhancements observed in highly skilled musicians. Our findings expose a new and unrecognized myogenic source to the FFR that drives its large inter-subject variability and cast doubt on whether changes in the response typically attributed to neuroplasticity/pathology are solely of brain origin.

Keywords: Auditory brainstem response (ABR); auditory evoked potentials (AEPs); post-auricular muscle reflex (PAMR)

Introduction

Neuroelectric brain recordings have been indispensable in demonstrating neuroplasticity at all levels of the auditory system. In particular, the frequency-following response (FFR), a scalp-recorded neurophonic reflecting phase-locked activity along the auditory neuroaxis to periodic signals, has served as a “neural fingerprint” of sound coding in the EEG (Kraus et al., 2010). The precision of the FFR is evidenced by the fact these brain potentials can support intelligible speech when they are replayed (i.e., sonified) as audio stimuli (Bidelman, 2018a). The strength to which FFRs capture voice pitch (i.e., fundamental frequency; F0) and harmonic timbre cues of complex signals is also causally related to listeners’ perception of speech material (Weiss et al., 2015). FFRs are also enhanced by various experiential factors including native language experience (Krishnan et al., 2010; Zhao et al., 2018), musical abilities (Mankel et al., 2018; Wong et al., 2007), and perceptual learning (Reetzke et al., 2018). Conversely, FFRs reveal deficiencies in neural processing in a variety of auditory, literacy, and neurodevelopmental disorders (e.g., dyslexia, autism, hearing loss, aging; Anderson et al., 2013; Bidelman et al., 2017a; Chandrasekaran et al., 2009; Russo et al., 2008; White-Schwoch et al., 2015). Collectively, a wealth of studies implies FFRs might be a valuable auditory biomarker for tracking both positive and maladaptive auditory plasticity in the brain that either bolsters or compromises the perceptual organization of speech and musical sounds.

Despite an abundance of FFR studies and potential applications to understanding brain plasticity and normal and disordered central auditory processing, the anatomical origins of the FFR remain highly contentious (Bidelman, 2018b; Coffey et al., 2016; Coffey et al., 2019; Holmes et al., 2017; White-Schwoch et al., 2019). Historically described as a brainstem potential (Chandrasekaran et al., 2010; Smith et al., 1975; Sohmer et al., 1977), it is now recognized FFRs reflect a mixture of phase-locked activity from brainstem and cortical structures throughout the auditory pathway (Bidelman, 2018b; Coffey et al., 2019). While different neuroimaging techniques emphasize brainstem- and cortico-centric contributions to the response, the FFR has always been described, unequivocally, as a *brain response* of *auditory-neurogenic* origin (Bidelman et al., 2018; Chandrasekaran et al., 2010; Hoormann et al., 1992). However, anecdotal observations over the past decade reveal occasional listeners that produce unusually large FFRs that far exceed the amplitudes expected for an auditory-neurogenic potential in humans. Such enigmatic responses are easily obscured in grand average data but can differ from the FFRs’ normal operating range (Chandrasekaran et al., 2010) by an order of magnitude (i.e., 1-2 µV vs. 100-200 nV range), and thus warrant further

explanation. Here, we expose a heretofore unrecognized *myogenic* source of the FFR that explains substantial individual differences in the response including waveform enhancements usually attributed to plasticity in central auditory nervous system function (Coffey et al., 2017; Kraus et al., 2009; Kraus et al., 2014; Krishnan et al., 2005; Krizman et al., 2012; Mankel et al., 2018; Musacchia et al., 2007; Parbery-Clark et al., 2009; Wong et al., 2007; Zhao et al., 2018).

Situated behind the ear, the postauricular muscle (PAM) is part of a vestigial startle reflex that once acted to retract the pinna to protect hearing (Bérzin et al., 1993). The muscle produces large (>100 µV), bilateral contraction with peak latency of 9-15 ms following brief sounds (O'Beirne et al., 1999; Thornton, 1975) and is highly variable across listeners (Picton et al., 1974). Anesthetic blockage of the muscle and facial nerve abolishes PAM confirming its non-neural origin (Bickford et al., 1964). While PAM activation declines with increasing stimulus rates (Geisler et al., 1958), the reflex can be elicited by surprisingly fast periodic stimuli without fatigue or habituation (Jacobson et al., 1964) ((but see Yoshie et al., 1969)). Indeed, motor units underlying the PAM reflex can be driven at rates up to 100-200 Hz (Jacobson et al., 1964; Kiang et al., 1963), resulting in steady-state muscle potentials that, like the FFR, phase-lock to periodic signals (Kiang et al., 1963). Problematically, these rates closely coincide with the low-F0 (~100 Hz) pitched stimuli used in most auditory FFR studies (Coffey et al., 2016). This raises the possibility that FFRs to low-frequency sounds, including the voice pitch and low harmonics of speech, might be partially driven by muscular sources rather than auditory structures, *per se*. This is particularly relevant in the context of typical FFR recording approaches, which place electrodes behind the ear where PAM reflex is optimally recorded (O'Beirne et al., 1999). Indeed, in a survey of FFR studies over the past 50 years (N=314 studies), we found nearly half (42%=131 papers; see *SI Materials*) used a mastoid reference electrode montage that promotes extraneous pickup of PAM muscle artifact (**Fig. 1a**). The problem thus appears widespread in the literature. More critically, identifying undocumented muscular confound in the FFR would be particularly germane to interpreting plasticity studies and the unchallenged assumption that amplified FFRs (e.g., as in musicians, bilinguals) necessarily reflect increased fidelity of auditory neural coding due to listening experience ((cf. Bidelman et al., 2011; Coffey et al., 2017; Kraus et al., 2009; Krizman et al., 2012; Mankel et al., 2018; Musacchia et al., 2007; Parbery-Clark et al., 2009; Wong et al., 2007; Zhao et al., 2018)).

Among the more widely reported neuroplastic effects captured in the FFR are the putative enhancements reported in musicians (Kraus et al., 2010; Musacchia et al., 2007; Schneider et al., 2002; Wong et al., 2007). Speech-FFRs are stronger and shorter in latency in musicians relative to their nonmusicians peers (Kraus et al., 2009; Parbery-Clark et al.,

2009), providing a neural account of their enhanced speech perception observed behaviorally. Such enhancements are typically interpreted as reflecting stronger neural representation for speech shaped by experience-dependent plasticity from the enriched sonic environment afforded by musical engagement (Herholz et al., 2012; Kraus et al., 2010; Wong et al., 2007). However, recent studies have challenged this notion by demonstrating even nonmusicians with superior music-listening abilities (i.e., “musical sleepers”) have “enhanced” FFRs that mirror those of highly trained musicians (Mankel et al., 2018). Such findings reveal innate differences in auditory brain function (and possibly other unmeasured factors) can easily masquerade as plasticity in studies on the brain benefits of music (Musacchia et al., 2007; Tierney et al., 2015; Wong et al., 2007). The present study was not intended to refute the possible connections between musicianship and FFR enhancements observed in both cross-sectional and longitudinal studies (Musacchia et al., 2007; Nan et al., 2018; Tierney et al., 2015; Wong et al., 2007). Rather, we aimed to identify whether PAM muscle activity naturally induced by sound stimulation might not only be larger in musicians but partially mediate the auditory processing enhancements reported in studies on music-related plasticity.

To this end, we evaluated whether unmeasured muscle artifact might explain substantial inter-subject variability in the FFR and account for at least some of the neural enhancements in speech processing frequently reported in highly skilled listeners (e.g., musicians). A major source of variation in the strength of PAM elicitation stems from uncontrolled eye movements (Patuzzi et al., 1999). Gaze directed toward the ear of sound presentation potentiates PAM contraction and thus pickup of the muscle artifact in EEG (O'Beirne et al., 1999; Patuzzi et al., 1999). By experimentally manipulating PAM with a gaze paradigm, we show here that repeated stimulation of the muscle produces “following-” like potentials in the EEG via simple linear superposition of overlapping PAM wavelets ((cf. Bidelman, 2015)). Moreover, we find this muscle noise easily masquerades as the auditory FFR and spuriously amplifies the response by 3-4x fold, partially accounting for FFR enhancements observed in highly skilled musicians. As a solution for recording artifact-free FFRs, we further show PAM-FFR contamination is easily circumvented by using high-frequency stimuli and relocating electrodes to a non-cephalic (neck) site.

Results

We measured postauricular muscle (PAM), click-evoked auditory brainstem responses (ABRs) and tone-evoked frequency-following response (FFR) potentials reflecting myogenic (PAM) and neurogenic (ABR/FFR) responses evoked by sound, respectively. The sample included young, normal hearing listeners with varying degrees of musical training to assess

whether putative enhancements in the FFR reported in experienced listeners ((cf. Mankel et al., 2018; Musacchia et al., 2007; Skoe et al., 2012; Wong et al., 2007)) might instead result from undocumented PAM muscle artifact rather than auditory neuroplasticity.

Postauricular muscle (PAM) artifact is present but variable across ears. We first confirmed PAM could be successfully elicited in individual ears and experimentally manipulated by directing listeners' eye gaze towards their stimulated ear (**Fig. 1b**). **Figure 1c** shows grand average click-ABRs recorded using montages with ipsilateral mastoid vs. midline (C7) electrode reference. In both traces, eye gaze was directed toward the right (ipsilateral) ear, which was expected to elicit maximal PAM contraction (O'Beirne et al., 1999; Patuzzi et al., 1999). Positive deflections in the first 6 ms form the canonical waves of the auditory brainstem response (I = 1.5 ms, III=3.5 ms, V=5.5 ms) reflecting serial activation of the major nuclei along the ascending auditory pathway. Following the ABR, the myogenic PAM artifact was evident between 12.5-15 ms and was especially prominent in mastoid-referenced recordings (i.e., Fpz – M2). PAM artifact was not evident at C7 where the reference electrode is distanced from the muscle. Consequently, PAM artifact was easily isolated from the neurogenic ABR by simple waveform subtraction of mastoid vs. neck recordings (**Fig. 1d**). Although PAM artifact was present in all ears to some degree, the response was highly variable, ranging from 0.5-10 μV (peak-to-peak amplitude) across individuals.

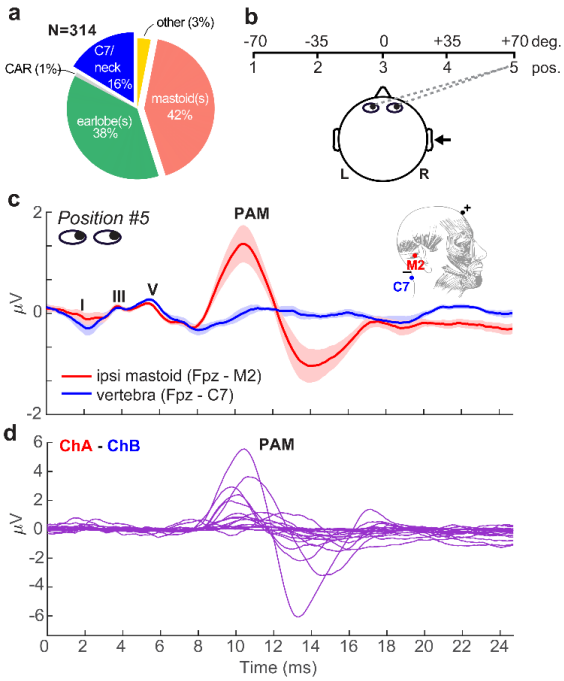

Figure 1: Eye gaze toward the ear introduces PAM artifact in ABRs. (**a**) In our literature review of N=314 FFR studies, nearly half (42%=131 papers) use a mastoid reference electrode montage that can promote inadvertent pickup of muscle artifact (see *SI Materials*). (**b**) Schematic of the visual gaze paradigm to direct listeners' eyes

during ABR/FFR recording. Listeners were positioned 1 m from the booth wall and were cued to direct their eye gaze to one of 5 positions spanning ±70 degrees from head center relative to the ipsilateral ear of stimulus presentation (right ear). **(c)** Grand average ABR waveforms recorded with a vertical ipsilateral montage between a non-inverting electrode at the high forehead (~Fpz) referenced to an inverting electrode placed on the (i) ipsilateral mastoid (M2) or (ii) 7th cervical vertebra (C7). Eye gaze was directed to position 5 (70 deg) in both cases. Strong PAM is recorded for the channel with electrode over the ipsilateral mastoid. Moving the reference to C7 (i.e., distal to the PAM muscle) eradicates pickup of the artifact. (**d**) Individual data, with PAM responses isolated via subtraction of the traces in panel C. PAM strength ranges from 0.5-10 μV (peak-to-peak) across individuals. Anatomy adapted from Feneis (1994). Shading = ± 1 s.e.m.

PAM contraction confounds the auditory FFR but declines with stimulus frequency and electrode montage. Having established PAM artifact was easily recordable and could be manipulated experimentally, we then tested whether FFR strength might also systematically vary with eye gaze direction and thus expose a myogenic source of the neural response. Confirming our intuition, FFRs to complex tones varied parametrically in amplitude when listeners were cued to direct their gaze across a ±70^0 range (**Fig. 2a**). Hard rotation of the eyes to either the left or right ear enhanced FFRs by 3-4x, particularly between 100-200 Hz where the PAM resides within the EEG spectrum (O'Beirne et al., 1999). FFR amplitude depended strongly on both eye gaze and recording location [position x channel: $F_{4,152.16}$ = 3.72, P = 0.0064; η_p^2 = 0.09]. For the mastoid channel, FFR strength decreased for gaze directed toward the midline (0^0) and increased with gaze toward either ear (quadratic contrast: t_{152}=6.82, P<0.0001). A nearly identical pattern was observed for the 200 Hz stimulus (data not shown; position x channel: $F_{1, 50.4}$ = 8.52, P = 0.0052; η_p^2 = 0.14). Moreover, a direct comparison of frequency effects revealed stronger FFRs in the 100 Hz vs. 200 Hz condition [main effect of frequency: $F_{1, 117.99}$ = 4.66, P = 0.033; η_p^2 = 0.04], indicating PAM-related changes in FFR declined with increasing stimulus frequency. Myogenic-induced enhancements were not apparent in electrodes positioned far from the mastoid and FFRs were invariant to eye gaze when recorded from the Fpz-C7 channel (linear and quadratic contrasts: P > 0.17) (**Fig. 2b**).

We also found PAM peak-to-peak amplitude was highly correlated with FFR root-mean-squared (rms) amplitude [Pearson's-r = 0.72, P = 0.0005] (**Fig. 2c**). This suggests listeners' FFR directly scaled with the size of their muscle artifact. Collectively, these findings reveal FFR strength depends critically on eye gaze position and moreover, that PAM activity overlays true neural responses, potentially masquerading as the neurophonic FFR commonly described as having brainstem origin (Bidelman, 2018b; Chandrasekaran et al., 2010; Coffey et al., 2019).

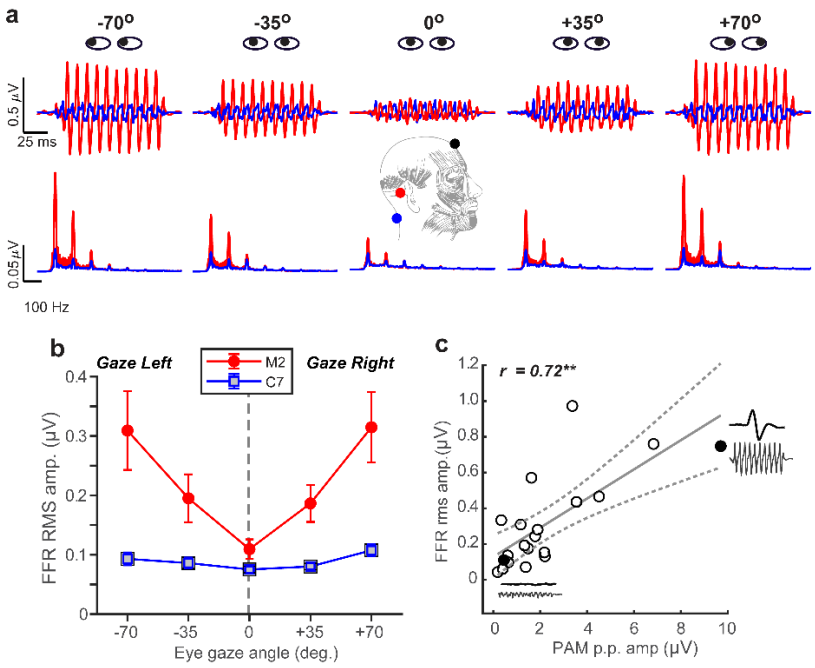

Figure 2: FFR strength systematically scales with the degree of PAM activation. (a) FFR time waveforms (*top*) and spectra (*bottom*) as a function of eye gaze spanning from left to right ear. Note the strong fundamental and integer-related harmonic frequencies of the stimulus F0=100 Hz (200 Hz condition not shown). (**b**) FFR amplitude systematically increases when gaze is directed away from the midline (in either ipsi or contra direction) for mastoid-referenced recordings. FFR amplitude is invariant to eye gaze in recordings referenced to C7, suggesting a midline montage (i.e., Fpz- C7) eradicates PAM artifact. (**c**) Correlation between PAM peak-to-peak (Fig. 1a) and FFR rms amplitudes recorded with hard right eye gaze (position #5). Solid points reflect representative subjects whose raw waveforms are shown in the insets. Dotted lines = 95% CI; errorbars= ± 1 s.e.m.; $^{**}P < 0.01$

Sustained FFRs are explained by serial PAM contractions: Model simulations. Single-unit motor neurons underlying the PAM reflex can be driven at rates up to 100-200 Hz (Jacobson et al., 1964; Kiang et al., 1963). This raises the possibility that the FFR, and what appears to be a sustained brain potential, might instead reflect a series of overlapping transient PAM artifacts evoked by the individual pitch pulses of low-frequency, periodic sounds. To test this possibility, we simulated FFRs via simple convolution of listeners' isolated PAM response (i.e., Fig. 1) with a 100 Hz impulse train. This train had identical periodicity as the complex tones used in our FFR experiment. This model regenerates the PAM at each pitch period of the F0, such that responses temporally overlap and produce a quasi-steady state auditory response (Galambos et al., 1981). Repeating the PAM wavelet across time (**Fig. 3a**) yielded a sustained waveform that was strikingly similar to the empirical FFR recordings (**Fig. 3b**). Actual and PAM-derived FFRs were highly correlated (r_{xcorr} = 0.71 ± 0.21; *inset*), suggesting upwards of 50.4% of the variance (R^2) in the FFR could be explained by a non-neuronal source.

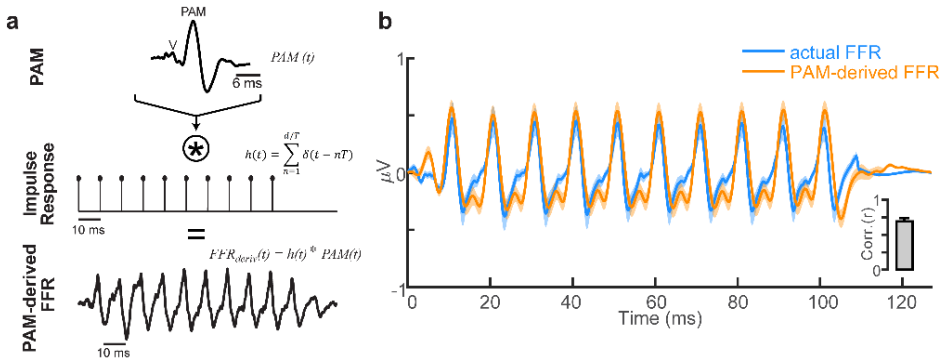

Figure 3: FFR waveforms can be explained as phase-locked PAM artifact. (a) Convolution model for generating the FFR based on repetition of the transient PAM response (a muscle artifact) (for details, see Bidelman, 2015). FFRs generated by a complex tone with period *T* are conceived as a convolution of the PAM artifact (*PAM(t),* top row) with the individual pitch periods of the tone, modeled as a periodic pulse train (*h(t*),middle row). The resulting derived FFR ($FFR_{deriv}(t)$, bottom row) is generated by a series of overlapping transient PAMs at the periodicity of the impulse train *T* = 10 ms (i.e., F0 = 100 Hz). **(b)** Comparison of empirical FFR recordings (F0=100 Hz complex tone stimulus) and simulated FFRs, derived via the convolution of PAM attract with the stimulus F0 periodicity. FFR traces reflect responses recorded with eye gaze directed at position #5 (see Fig. 1) and contain significant PAM. A series of temporally overlapping PAM wavelets repeated at the F0 of a tone accounts for ~50% of the variance in actual FFRs (*inset*). shading/errorbars = ±1 s.e.m.

PAM artifact mediates music-related plasticity in FFRs. Having established that FFRs are partly confounded by muscular influences, we next asked whether putative enhancements reported in the literature (e.g., due to musical training, bilingualism (Krishnan et al., 2005; Krizman et al., 2012; Mankel et al., 2018; Musacchia et al., 2007; Skoe et al., 2012; Wong et al., 2007)) might be explained not in terms of auditory plasticity but rather, differences in tonic PAM contraction among listeners. To this end, we conducted multiple regression analyses to assess whether a linear combination of listeners' neuro-behavioral measures (i.e., years of music training, PAM amplitudes) predicted the strength of their FFR [e.g., FFR_{rms}~ music*PAM]. **Figure 4** shows leverage plots (Sall, 1990) illustrating the relative effects of music training and PAM artifact amplitudes on FFR strength. Variance inflation factors (VIFs) were < 2 for both predictor variables, indicating negligible multicollinearity in the data (Lüdecke, 2020). We found that music training strongly predicted FFR strength [r = 0.34, P = 0.00076] (**Fig. 4a**), consistent with prior studies suggesting musicianship enhances the brain's early neural encoding of complex sounds ((cf. Mankel et al., 2018; Musacchia et al., 2007; Skoe et al., 2012; Wong et al., 2007)). However, even after partialing out musical training, the strength of listeners' PAM remained strongly correlated with FFR amplitude [r = 0.49, P < 0.0001] (**Fig. 4b**). Similarly, musicianship was independently correlated with enhanced FFR amplitudes after controlling PAM contributions [r = 0.21, P = 0.037]. Indeed, a regression model that included the interaction between music training and PAM amplitudes was a significant improvement in describing FFR variance over one containing music alone [$F_{1,92}$ =

29.01, $P < 0.001$]. Taken together, these data confirm that the strength of the FFR is driven by an interaction between neuroplasticity (i.e., related to listening experience) and artifactual origins.

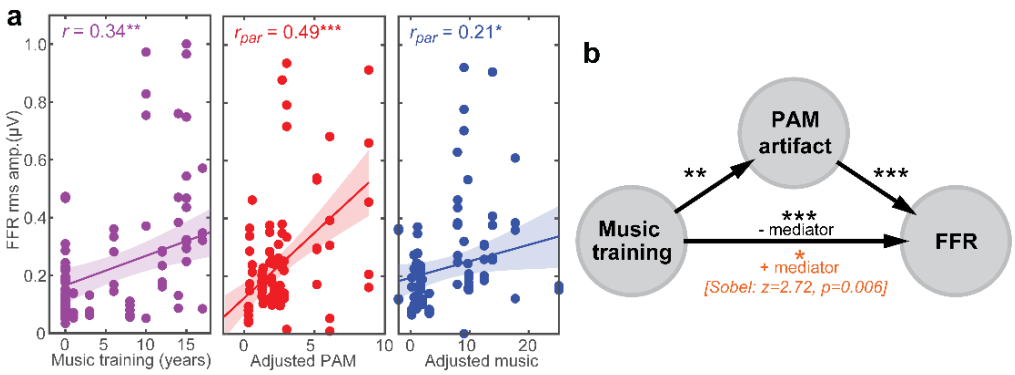

Figure 4: PAM artifact can masquerade as experience-dependent plasticity in the FFR. (**a**) (*left*) FFR is stronger in listeners with more musical training, suggestive of the experience-dependent plasticity reported in trained musicians ((cf. Mankel et al., 2018; Musacchia et al., 2007; Skoe et al., 2012; Wong et al., 2007)). Both PAM (*middle*) and musical training (*right*) independently correlate with FFR strength after partialing out the other variable. Correlation data are aggregated from the 5 eye gaze positions. (**b**) Mediation analysis. The putative FFR-music relation is severely reduced after accounting for PAM [Sobel test: z=2.72, P=0.006] suggesting uncontrolled muscle artifact partially mediates the relation between musical training and FFR. Shading = 95% CI; *P<0.05, **P<0.01, ***P<0.001.

To further evaluate the confounding link between PAM-related muscle noise and putative music-induced FFR plasticity (e.g., Mankel et al., 2018; Musacchia et al., 2007; Skoe et al., 2012; Wong et al., 2007), we conducted mediation analyses (Preacher et al., 2004; Sobel, 1982) to determine the degree to which PAM artifact mediated FFR strength (**Fig. 4b**). Mediation contrasts the strength of regressions between a pairwise vs. triplet (mediation) model (i.e., $X \rightarrow Y$ vs. $X \rightarrow M \rightarrow Y$). Mediator M is said to mediate the relation between the $X \rightarrow Y$ if (i) X first predicts Y on its own, (ii) X predicts M, and (iii) the functional relation between $X \rightarrow Y$ is rendered insignificant after controlling for M (Preacher et al., 2004). We found PAM satisfied the first two criteria for a mediating variable (**Fig. 4b**). However, accounting for the strength of listeners' PAM artifact severely reduced—but did not render insignificant—relations between music training and FFR strength (Sobel test: z=2.72, P=0.006) (Sobel, 1982). These results suggest PAM artifact is a partial (but not fully) mediating variable describing music-related enhancements observed in the FFR.

FFR timing is independent of PAM. The analyses thus far revealed links been amplitude properties of the FFR and PAM reflex. However, plasticity in the FFR has also been described in the latency of the response to speech and musical sounds, with faster neural timing following long-term musicianship (Bidelman et al., 2014; Mankel et al., 2018; Parbery-Clark et al., 2012) and short-term auditory training (Anderson et al., 2013). To explore the possibility

that variation in FFR timing might also be due to undocumented PAM artifact, we examined correlations between the onset latency of the FFR [measure in the 6-12 ms search window (Mankel et al., 2018)] and PAM artifact [8-18 ms; see Fig. 1d]. However, neither latency [r = -0.10, P = 0.69] nor amplitude [r = 0.14, P = 0.57] of the PAM predicted FFR timing to the 100 Hz stimuli. Similar null correspondence was observed at 200 Hz [all Ps > 0.09]. Thus, in stark contrast to FFR amplitude measures, fine timing precision of the FFR appears less susceptible to artifactual influence.

Discussion

Our findings expose a previously undocumented influence of myogenic origin to the auditory FFR. This study, to the best of our knowledge, is the first to explicitly show an electromyographic (muscle) rather than electroencephalographic (brain) contribution to the FFR. We demonstrate uncontrolled eye gaze systematically alters the apparent strength of FFRs with tandem PAM contraction. More critically, we show this muscular noise can easily masquerade as neural enhancements, accounting for large variability in the response previously ascribed to auditory-sensory plasticity. Importantly, these data do not negate the possibility that certain human experiences (e.g., music training, language expertise, learning) can confer experience-dependent plasticity that manifests in spectrotemporal changes in the FFR (Kraus et al., 2014; Krishnan et al., 2005; Mankel et al., 2018). Rather, we argue that undue muscle confounds external to the brain may play a larger role in generating the FFR and its use as a biomarker of plasticity than conventionally thought.

While typically considered an artifactual nuisance to auditory EEG and evoked potential recordings, the PAM and related myogenic potentials do find several important neuro-otological applications including hearing threshold (Yoshie et al., 1969) and vestibular assessment (Rosengren et al., 2019). Yet, in the context of FFRs whose purpose is to evaluate central auditory neural processing and the brain's sensory representation of complex sounds, we show concomitant PAM muscle activation easily confounds these neurogenic responses, spuriously amplifying the FFR by 3-4x fold. Our findings are reminiscent of other microflexes shown to confound oscillatory EEG responses ((e.g., microsaddes Yuval-Greenberg et al., 2008)) and suggest uncontrolled eye movements can systematically alter sustained auditory FFR potentials via PAM muscle engagement.

We found PAM-related artifact was largest for hard rotation of the eyes toward or way from the ipsilateral ear of sound presentation but parametrically scaled in direct portion with listeners' lateral eye gaze. This point is particularly salient in light of speech-FFR studies that use passive listening paradigms where listeners are allowed to watch muted subtitled

movies(Coffey et al., 2016; Mankel et al., 2018; Price et al., 2021; Wong et al., 2007). Videos are thought to provide added control during electrophysiological procedures, inducing a calm yet wakeful state that yields cleaner electrophysiological recordings (Coffey et al., 2016; Wong et al., 2007). However, subtended gaze angles when viewing a monitor at typical seated distance can exceed ~30-35 degrees (Feng et al., 2008). Our data clearly show the FFR is nearly double its nominal size at these viewing angles (Fig. 2b). Consequently, while seemingly an innocuous control task, undue eye movements during video watching could easily confound the FFR by artificially inflating response amplitude. Along these lines, there is evidence that musicians show reduced fixation dwell times and more saccades during viewing tasks (Perra et al., 2022). Such increased eye movement could explain the larger PAM activation (and artifactual FFR) we find in musically trained individuals (Fig. 4). Similar augments could extend to bilinguals, who also show increased visual search (Ratiu et al., 2017) and more robust speech FFRs (Krishnan et al., 2005; Krizman et al., 2012).

While there is overwhelming evidence in humans and animals to suggest PAM artifact is generated from the bipolar activation of muscle fibers behind the auricle of the ear(Kiang et al., 1963; O'Beirne et al., 1999; Patuzzi et al., 1999), it is conceivable that other non-auditory mechanisms contribute to FFR contamination. For example, it is well know that FFRs require delicate recording strategies to prevent inadvertent pickup of stimulus headphone artifact that can easily swamp the biological response (Price et al., 2021). Electromagnetic shielding (used here) prevents this possibility(Price et al., 2021) and can be further ruled out in the present data by the fact that FFRs showed gaze- and electrode-dependent changes that would not occur if waveforms were mere stimulus bleed (Fig. 2b). However, bogus FFR amplification could also result from other biological sources. Indeed, bone-conducted FFRs have been recorded in profoundly deaf listeners suggesting non-auditory pathways of response generation (Ribarić et al., 1984). These might include direct or indirect contributions from the vestibular system (e.g., evoked myogenic potentials(Lawlor et al., 2022; Prevec et al., 1996; Ribarić et al., 1984)) and/or somatosensory contributions near the electrode-skin interface which can persist up to rates of 287 (Lawlor et al., 2022) and 130 Hz (Prevec et al., 1996), respectively. Regardless of the underlying mechanism, our data clearly demonstrate physiological noise outside the auditory system easily conflates neurogenic FFR signals.

Several studies have shown enhanced voice pitch (F0) and timbre (harmonic) encoding in musically trained listeners (Kraus et al., 2010; Kraus et al., 2009; Mankel et al., 2018; Musacchia et al., 2007; Parbery-Clark et al., 2009; Wong et al., 2007), though not always consistently ((e.g., see Bidelman et al., 2015; Strait et al., 2012)). Our data confirm a robust and independent relation between musical training and the strength of listeners'

auditory FFR (Mankel et al., 2018; Musacchia et al., 2007; Skoe et al., 2012; Wong et al., 2007) (Fig. 4a). However, in a departure from prior studies, we show such effects are easily confounded. PAM contraction was both larger in listeners with more extended music training and partially mediated enhancements in their FFR (Fig. 4b). At first glance, these data therefore cast doubt on whether speech-FFR enhancements associated with musical training (and perhaps other experiential factors) are solely experience-driven ((cf. Herholz et al., 2012; Munte et al., 2002; Wong et al., 2007)) or even entirely auditory-neurogenic in nature. Undue PAM influence might explain why some studies fail to observe FFR advantages in musicians (Bidelman et al., 2015; MacLean et al., 2023; Strait et al., 2012). Nevertheless, we show that even after controlling for PAM, music training remains a robust predictor of FFR enhancements. This indicates musicianship independently bolsters the strength of the FFR and does so above and beyond any artifactual sources.

Surprisingly, we found musicians have stronger PAM vestigial muscle reflexes than their nonmusician peers. This finding broadly converges with notions that intense auditory experiences might fortify tonic engagement of reflexive pathways that provide feedback control to peripheral hearing processes (Bidelman et al., 2017b; Brashears et al., 2003). Still, it remains to be seen whether other long-term listening experiences that also enhance FFR similarly elevate PAM and account for neuroplastic effects observed in bilingualism and tone-language expertise (Krishnan et al., 2005; Krizman et al., 2012; Zhao et al., 2018). Regardless, the intrusive nature of PAM mandates caution for interpretating even short-term changes in the FFR, as observed in rapid perceptual learning studies (Anderson et al., 2013; Reetzke et al., 2018). More successful learners could show increased arousal while acquiring novel auditory information, leading to increased eye movements that exaggerate PAM artifact, and in turn false amplification of FFRs. FFRs are modulated by listeners' arousal state at the single-trial level (Carter et al., 2023; Lai et al., 2022) and eye movements change during the learning process(Laamerad et al., 2020). Thus, while it awaits empirical confirmation, our data raise the possibility that rapid plasticity observed in FFRs during short-term auditory/speech learning tasks might be due to not improvements in the brain's sensory representation of sound, *per se*, but an unmeasured artifactual source (Anderson et al., 2013; Reetzke et al., 2018).

Fortunately, our data offer a direct solution to easily thwart PAM-related confounds in the FFR and allow for untainted assessment of neuroplasticity. FFRs are frequently recorded using a differential electrode montage and non-inverting reference electrode placed on the bony mastoid process of the ipsilateral ear of stimulation (e.g., Fpz-M1/M2; see Fig. 1c, inset). We show this common practice is highly problematic, leading to extraneous pickup of the

adjacent PAM muscle and overinflation of FFR that, by our estimates, has affected nearly half the published literature (see Fig. 1a and *SI Materials*). Repositioning electrodes to the earlobe (another common technique) (Chandrasekaran et al., 2010; Skoe et al., 2010) attenuates but does not fully eliminate PAM pickup (O'Beirne et al., 1999). Instead, we find clean FFRs are easily recorded with electrodes placed on the upper neck (C7 vertebra), distal to the pinna and PAM muscle fibers. A midline Fpz-C7 montage has the further advantage that it (i) reduces pickup of more peripheral (cochlear) sources of the FFR and (ii) is optimally oriented with the vertical dipolar sources in the brainstem that dominate generation of the neurogenic FFR (Bidelman, 2015; Bidelman, 2018b; Galbraith et al., 2000). At present, it appears only 16% of studies use this optimal C7/neck montage (Fig. 1a). Additionally, we showed that FFR latency measures were largely independent of artifactual influences. Thus, timing characteristics of the FFR might provide a more veridical index of neuroplasticity (Anderson et al., 2013; Bidelman et al., 2014; Mankel et al., 2018; Parbery-Clark et al., 2012) than amplitude measures alone when tracking brain changes due to experience-dependent factors and novel sound learning (but see (Mankel et al., 2018)). Lastly, we found that PAM-related changes in FFR declined with increasing stimulus frequency. This suggests that in addition to isolating brainstem-centric sources of the response without cortical contributions (Bidelman, 2018b), the use of auditory stimuli with higher F0s (e.g., > 200 Hz) might be further advantageous in protecting against PAM confounds in the FFR.

In conclusion, our data provide new evidence that myogenic sources can artificially inflate the sound-evoked FFR and might account for certain *de novo* enhancements in the response. Provocatively, they also show that formally trained musicians have additional gains in sensory brain processing above and beyond PAM-related confounds. Our results emphasize the critical need for future studies to safeguard against ocular and myogenic confounders before claiming changes in FFR track with improvements in auditory brain function due to experience-dependent factors or neurobehavioral interventions. Of practical implication, we recommend that to measure true neurogenic FFRs without undue electromyographic contamination, investigators should (i) adopt a midline, necked-referenced recording approach, (ii) use high-frequency F0 stimuli (> 200 Hz) where PAM contributions are minimal, and (iii) focus primarily on response latency quantification to index disordered auditory processing and/or neuroplastic changes due to intervention.

Materials and Methods

Participants. The sample included N = 20 young adults (age [$\mu \pm \sigma$]: 24.9 ± 2.8 years; 4 male, 16 female). This sample size was determined *a priori* to match those of comparable studies on

auditory plasticity and the FFR (Bidelman et al., 2014; Coffey et al., 2016; Parbery-Clark et al., 2009). All had normal hearing (i.e., puretone air-conduction thresholds ≤ 25 dB HL; 250-8000 Hz), similar levels of education (19.1 ± 2.3 years), and reported no previous history of neuropsychiatric illness. All but one individual was right handed (77 ± 45% laterality) (Oldfield, 1971). The sample included a range of formal musical training ($\mu \pm \sigma$: 6.5 ± 7.3 years; range 0-23 years). Each gave written informed consent in compliance with a protocol approved by Indiana University IRB.

Stimuli*.* Auditory brainstem responses (ABRs) were recorded to 100 μs clicks. Frequency-following responses (FFRs) were elicited by complex pitches (periodic click trains) with fundamental frequencies (F0s) of either 100 or 200 Hz (Bidelman, 2015). Pulse trains (Dirac comb functions) were constructed using a periodic series of impulses $h(t) = \sum_{n=1}^{\frac{d}{T}} \delta(t - nT)$, where *d* is the duration of the desired pulse train (here, 100 ms), and *T* is the period between successive impulses (i.e., the pitch period = 1/F0)**.** Each pulse of the train was constructed using identical clicks (bandwidth, pulse with, amplitude) to those described for eliciting the ABR, spaced with F0s of 100 and 200 Hz. This allowed us to directly test the assumption that a large amplitude periodic FFR response is a linear superposition of repeated transient PAM waves ((cf. Bidelman, 2015)).

EEG recordings*.* Participants sat in an electro-acoustically shielded booth in a recliner chair positioned 1 m from the wall. Numbered signs (labeled 1-5) were positioned in the front hemifield demarcating angles of -70, -35, 0, +35, +70 degrees (left to right) relative to head center (see **Fig. 1b**). For each condition, we directed participants' eye gaze to one of the five angles by cueing the respective number. Compliance was monitored by the experimenter via a window into the chamber. FFRs were recorded with eye gaze directed at each of the 5 azimuths.

FFRs were recorded using a two-channel vertical montage with Ag/AgCl disc electrodes placed on the mid-hairline (i.e., midway between Fpz and Fz) referenced to (i) right (ipsi) mastoid (M2) and (ii) 7th cervical vertebra (mid-forehead= ground). Due to technical error, data from the second channel were not recorded in N=2 listeners and were treated as missing values. Impedances were ≤ 5 kΩ. EEGs were digitized at 20 kHz using a SmartEP EEG system (Intelligent Hearing Systems; Miami, FL) with an online passband of 50 - 3000 Hz (+ 60 Hz notch filter) and 100K amplifier gain. Evoked responses were elicited from each participant in response to right ear presentation at 80 dB SPL through electromagnetically shielded insert earphones (Ultra-shielded ER3A inserts, 300Ω; IHS, Miami, FL) that eradicated electromagnetic stimulus artifact from contaminating biological responses (Price et al., 2021).

Stimuli were presented with fixed, rarefaction polarity at a repetition rate of 9.09/s. Presentation order was randomized both within and across participants. Continuous EEGs were epoched (*ABR*: 0-24.7 ms; *FFR:* 0-127 ms) and ensemble averaged across trials to derive evoked responses per condition. Sweeps > ±50 µV were automatically rejected during online averaging. A total of 2000 artifact-free sweeps were collected per stimulus and eye gaze position.

Model simulating FFRs from PAM artifact*.* To evaluate the degree to which FFRs are explained by PAM artifact, we compared the empirical FFR recordings with derived FFRs, simulated via simple convolution (e.g., Bidelman, 2015; Carter et al., 2023; Goldstein et al., 1958; Janssen et al., 1991). The model presumes the sustained following response is generated by a series of overlapping onset responses such that the FFR is an iterated ABR/PAM ((see Fig. 1 in Bidelman, 2015)). We simulated FFRs by convolving each listener's PAM-contaminated ABR (see Fig. 1) with a periodic click train of 100 Hz spacing (i.e., the FFR stimulus F0). This process generated a new ABR/PAM signature at each stimulus pulse which when strung across time, yielded a complex waveform closely mirroring the actual FFR. We then assessed correspondence between model-predicted and true FFR recordings via cross-correlation (20 ms lag search window) (Bidelman, 2015; Galbraith et al., 2000).

Statistical analysis*.* We analyzed the data using a 2x2 mixed-model ANOVA in *R* ((R Core Team, 2020)) and the *lme4* package (Bates et al., 2015). Fixed effects were eye gaze position (5 levels) and channel montage (2 levels). Subjects served as a random effect. We used Satterthwaite's method to compute degrees of freedom. The data were SQRT-transformed to improve normality and homogeneity of variance assumptions necessary for parametric analyses. Effect sizes are reported as η_p^2.

We conducted regression analyses to assess whether a linear combination of listeners' neuro-behavioral measures (i.e., years of music training, PAM amplitudes) predicted the strength of their FFR [e.g., FFR_{rms}~ music*PAM]. We then used leverage plots (Sall, 1990), partial correlations to assess the relative strength of music vs. artifact regressors in driving putative musicianship-FFR relations (e.g., Mankel et al., 2018; Musacchia et al., 2007; Skoe et al., 2012; Wong et al., 2007). We used mediation analyses to evaluate relationships between neural and behavioral measures. We used an efficient, bootstrapping implementation of the Sobel statistic (Preacher et al., 2004; Sobel, 1982) (N = 1000 resamples) to determine whether PAM artifact fully or partially mediates the strength of listeners' FFR. The Sobel test contrasts the strength of regressions between a pairwise vs. triplet (mediation) model (i.e., *X→Y* vs. *X→M→Y).* Mediator *M* is said to mediate the relation between the *X→Y* if (i) *X* first

predicts *Y* on its own, (ii) *X* predicts *M*, and (iii) the functional relation between $X \rightarrow Y$ is rendered insignificant after controlling for *M* (Preacher et al., 2004).

Acknowledgments

Work supported by the National Institutes of Health (NIH/NIDCD R01DC016267).

Data availability

Data are available by request from the corresponding author.

Competing interests

The authors declare no competing financial interests.

References

Anderson, S., White-Schwoch, T., Parbery-Clark, A., Kraus, N. 2013. Reversal of age-related neural timing delays with training. Proceedings of the National Academy of Sciences of the United States of America 110, 4357-62.

Bates, D., Mächler, M., Bolker, B., Walker, S. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67, 1-48.

Bérzin, F., Fortinguerra, C.R. 1993. EMG study of the anterior, superior and posterior auricular muscles in man. Ann Anat 175, 195-7.

Bickford, R.G., Jacobson, J.L., Cody, D.T. 1964. Nature of average evoked potentials to sound and other stimuli in man. Annals of the New York Academy of Sciences 112, 204-23.

Bidelman, G., Powers, L. 2018. Response properties of the human frequency-following response (FFR) to speech and non-speech sounds: level dependence, adaptation and phase-locking limits. International Journal of Audiology 57, 665–672.

Bidelman, G.M. 2015. Multichannel recordings of the human brainstem frequency-following response: Scalp topography, source generators, and distinctions from the transient ABR. Hearing Research 323, 68-80.

Bidelman, G.M. 2018a. Sonification of scalp-recorded frequency-following responses (FFRs) offers improved response detection over conventional statistical metrics. Journal of Neuroscience Methods 293, 59-66.

Bidelman, G.M. 2018b. Subcortical sources dominate the neuroelectric auditory frequency-following response to speech. NeuroImage 175, 56–69.

Bidelman, G.M., Alain, C. 2015. Musical training orchestrates coordinated neuroplasticity in auditory brainstem and cortex to counteract age-related declines in categorical vowel perception. Journal of Neuroscience 35, 1240 –1249.

Bidelman, G.M., Gandour, J.T., Krishnan, A. 2011. Cross-domain effects of music and language experience on the representation of pitch in the human auditory brainstem. Journal of Cognitive Neuroscience 23, 425-34.

Bidelman, G.M., Weiss, M.W., Moreno, S., Alain, C. 2014. Coordinated plasticity in brainstem and auditory cortex contributes to enhanced categorical speech perception in musicians. European Journal of Neuroscience 40, 2662-2673.

Bidelman, G.M., Lowther, J.E., Tak, S.H., Alain, C. 2017a. Mild cognitive impairment is characterized by deficient hierarchical speech coding between auditory brainstem and cortex. Journal of Neuroscience 37, 3610-3620.

Bidelman, G.M., Schneider, A.D., Heitzmann, V.R., Bhagat, S.P. 2017b. Musicianship enhances ipsilateral and contralateral efferent gain control to the cochlea. Hearing Research 344, 275-283.

Brashears, S.M., Morlet, T.G., Berlin, C.I., Hood, L.J. 2003. Olivocochlear efferent suppression in classical musicians. Journal of the American Academy of Audiology 14, 314-24.

Carter, J.A., Bidelman, G.M. 2023. Perceptual warping exposes categorical representations for speech in human brainstem responses. NeuroImage 269, 119899.

Chandrasekaran, B., Kraus, N. 2010. The scalp-recorded brainstem response to speech: Neural origins and plasticity. Psychophysiology 47, 236-46.

Chandrasekaran, B., Hornickel, J., Skoe, E., Nicol, T., Kraus, N. 2009. Context-dependent encoding in the human auditory brainstem relates to hearing speech in noise: Implications for developmental dyslexia. Neuron 64, 311-9.

Coffey, E.B., Herholz, S.C., Chepesiuk, A.M., Baillet, S., Zatorre, R.J. 2016. Cortical contributions to the auditory frequency-following response revealed by MEG. Nature Communications 7, 11070.

Coffey, E.B.J., Chepesiuk, A.M.P., Herholz, S.C., Baillet, S., Zatorre, R.J. 2017. Neural correlates of early sound encoding and their relationship to speech-in-noise perception. Frontiers in Neuroscience 11.

Coffey, E.B.J., Nicol, T., White-Schwoch, T., Chandrasekaran, B., Krizman, J., Skoe, E., Zatorre, R.J., Kraus, N. 2019. Evolving perspectives on the sources of the frequency-following response. Nature Communications 10, 5036.

Feneis, H. 1994. Pocket Atlas of Human Anatomy. 3rd ed. Thieme Publishing Group.

Feng, J., Spence, I. 2008. Attending to large dynamic displays, CHI '08 Extended Abstracts on Human Factors in Computing Systems. Association for Computing Machinery, Florence, Italy. pp. 2745–2750.

Galambos, R., Makeig, S., Talmachoff, P.J. 1981. A 40-Hz auditory potential recorded from the human scalp. Proceedings of the National Academy of Sciences of the United States of America 78, 2643-7.

Galbraith, G., Threadgill, M., Hemsley, J., Salour, K., Songdej, N., Ton, J., Cheung, L. 2000. Putative measure of peripheral and brainstem frequency-following in humans. Neuroscience Letters 292, 123-127.

Geisler, C.D., Frishkopf, L.S., Rosenblith, W.A. 1958. Extracranial responses to acoustic clicks in man. Science 128, 1210-1.

Goldstein, M.H., Kiang, N.Y.S. 1958. Synchrony of neural activity in electric responses evoked by transient acoustic stimuli. Journal of the Acoustical Society of America 30, 107–114.

Herholz, S.C., Zatorre, R.J. 2012. Musical training as a framework for brain plasticity: Behavior, function, and structure. Neuron 76, 486-502.

Holmes, E., Herrmann, B. 2017. Revisiting the contribution of auditory cortex to frequency-following responses. Journal of Neuroscience 37, 5218-5220.

Hoormann, J., Falkenstein, M., Hohnsbein, J., Blanke, L. 1992. The human frequency-following response (FFR): Normal variability and relation to the click-evoked brainstem response. Hearing Research 59, 179-188.

Jacobson, J.L., Cody, D.T., Lambert, E.H., Bickford, R.G. 1964. Physiological Properties of the Post-Auricular Responses (Sonomotor) in Man. The Physiologist 7, 167-167.

Janssen, T., Steinhoff, H.J., Böhnke, F. 1991. Zum entstehungsmechanismus der frequenzfolgepotentiale. Otorhinolaryngol. Nova 1, 16-24.

Kiang, N.Y., Crist, A.H., French, M.A., Edwards, A.G. 1963. Postauricular electrical response to acoustic stimuli in humans. Massachusetts Institute of Technology Quarterly Progress Report No. 68, 218-225.

Kraus, N., Chandrasekaran, B. 2010. Music training for the development of auditory skills. Nature Reviews Neuroscience 11, 599-605.

Kraus, N., Skoe, E., Parbery-Clark, A., Ashley, R. 2009. Experience-induced malleability in neural encoding of pitch, timbre, and timing. Annals of the New York Academy of Sciences 1169, 543-57.

Kraus, N., Slater, J., Thompson, E.C., Hornickel, J., Strait, D.L., Nicol, T., White-Schwoch, T. 2014. Music enrichment programs improve the neural encoding of speech in at-risk children. Journal of Neuroscience 34, 11913-11918.

Krishnan, A., Gandour, J.T., Bidelman, G.M. 2010. The effects of tone language experience on pitch processing in the brainstem. Journal of Neurolinguistics 23, 81-95.

Krishnan, A., Xu, Y., Gandour, J.T., Cariani, P. 2005. Encoding of pitch in the human brainstem is sensitive to language experience. Brain Research Cognitive Brain Research 25, 161-8.

Krizman, J., Marian, V., Shook, A., Skoe, E., Kraus, N. 2012. Subcortical encoding of sound is enhanced in bilinguals and relates to executive function advantages. Proceedings of the National Academy of Sciences of the United States of America 109, 7877-81.

Laamerad, P., Guitton, D., Pack, C.C. 2020. Eye movements shape visual learning. Proc Natl Acad Sci U S A 117, 8203-8211.

Lai, J., Price, C.N., Bidelman, G.M. 2022. Brainstem speech encoding is dynamically shaped online by fluctuations in cortical α state. NeuroImage 263, 119627.

Lawlor, K.J., Clinard, C.G., Piker, E.G. 2022. Temporal Modulation Transfer Functions of Amplitude-Modulated Cervical Vestibular-Evoked Myogenic Potentials in Young Adults. Ear and Hearing 43.

Lüdecke, D. 2020. sjPlot: Data visualization for statistics in social science. R package version 2.8.6. https://CRAN.R-project.org/package=sjPlot.

MacLean, J.A., Stirn, J.R., Sisson, A.E., Bidelman, G.M. 2023. Short- and long-term experience-dependent neuroplasticity interact during the perceptual learning of concurrent speech. bioRxiv [preprint].

Mankel, K., Bidelman, G.M. 2018. Inherent auditory skills rather than formal music training shape the neural encoding of speech. Proceedings of the National Academy of Sciences of the United States of America 115, 13129-13134.

Munte, T.F., Altenmuller, E., Jancke, L. 2002. The musician's brain as a model of neuroplasticity. Nature Reviews Neuroscience 3, 473-8.

Musacchia, G., Sams, M., Skoe, E., Kraus, N. 2007. Musicians have enhanced subcortical auditory and audiovisual processing of speech and music. Proceedings of the National Academy of Sciences of the United States of America 104, 15894-8.

Nan, Y., Liu, L., Geiser, E., Shu, H., Gong, C.C., Dong, Q., Gabrieli, J.D.E., Desimone, R. 2018. Piano training enhances the neural processing of pitch and improves speech perception in Mandarin-speaking children. Proceedings of the National Academy of Sciences of the United States of America 115, E6630-E6639.

O'Beirne, G.A., Patuzzi, R.B. 1999. Basic properties of the sound-evoked post-auricular muscle response (PAMR). Hearing Research 138, 115-132.

Oldfield, R.C. 1971. The assessment and analysis of handedness: The Edinburgh inventory. Neuropsychologia 9, 97-113.

Parbery-Clark, A., Skoe, E., Kraus, N. 2009. Musical experience limits the degradative effects of background noise on the neural processing of sound. Journal of Neuroscience 29, 14100-7.

Parbery-Clark, A., Anderson, S., Hittner, E., Kraus, N. 2012. Musical experience offsets age-related delays in neural timing. Neurobiology of aging 33, 1483 e1-4.

Patuzzi, R.B., O'Beirne, G.A. 1999. Effects of eye rotation on the sound-evoked post-auricular muscle response (PAMR). Hearing Research 138, 133-46.

Perra, J., Latimier, A., Poulin-Charronnat, B., Baccino, T., Drai-Zerbib, V. 2022. A Meta-analysis on the Effect of Expertise on Eye Movements during Music Reading. J Eye Mov Res 15.

Picton, T.W., Hillyard, S.A., Krausz, H.I., Galambos, R. 1974. Human auditory evoked potentials. I. Evaluation of components. Electroencephalography and Clinical Neurophysiology 36, 179-90.

Preacher, K.J., Hayes, A.F. 2004. SPSS and SAS procedures for estimating indirect effects in simple mediation models. Behavior Research Methods, Instruments, & Computers 36, 717-731.

Prevec, T.S., Ribarić-Jankes, K. 1996. Can somatosensory system generate frequency following response? Pflugers Arch 431, R301-2.

Price, C.N., Bidelman, G.M. 2021. Attention reinforces human corticofugal system to aid speech perception in noise. NeuroImage 235, 118014.

R-Core-Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Ratiu, I., Hout, M.C., Walenchok, S.C., Azuma, T., Goldinger, S.D. 2017. Comparing visual search and eye movements in bilinguals and monolinguals. Attention, Perception, & Psychophysics 79, 1695-1725.

Reetzke, R., Xie, Z., Llanos, F., Chandrasekaran, B. 2018. Tracing the trajectory of sensory plasticity across different stages of speech learning in adulthood. Current Biology 28, 1419-1427.e4.

Ribarić, K., Prevec, T.S., Kozina, V. 1984. Frequency-following response evoked by acoustic stimuli in normal and profoundly deaf subjects. Audiology 23, 388-400.

Rosengren, S.M., Colebatch, J.G., Young, A.S., Govender, S., Welgampola, M.S. 2019. Vestibular evoked myogenic potentials in practice: Methods, pitfalls and clinical applications. Clin Neurophysiol Pract 4, 47-68.

Russo, N.M., Skoe, E., Trommer, B., Nicol, T., Zecker, S., Bradlow, A., Kraus, N. 2008. Deficient brainstem encoding of pitch in children with autism spectrum disorders. Clinical Neurophysiology 119, 1720-1731.

Sall, J. 1990. Leverage Plots for General Linear Hypotheses. The American Statistician 44, 308-315.

Schneider, P., Scherg, M., Dosch, H.G., Specht, H.J., Gutschalk, A., Rupp, A. 2002. Morphology of Heschl's gyrus reflects enhanced activation in the auditory cortex of musicians. Nature Neuroscience 5, 688-94.

Skoe, E., Kraus, N. 2010. Auditory brain stem response to complex sounds: A tutorial. Ear and Hearing 31, 302-24.

Skoe, E., Kraus, N. 2012. A little goes a long way: How the adult brain is shaped by musical training in childhood. Journal of Neuroscience 32, 11507-10.

Smith, J.C., Marsh, J.T., Brown, W.S. 1975. Far-field recorded frequency-following responses: Evidence for the locus of brainstem sources. Electroencephalography and Clinical Neurophysiology 39, 465-72.

Sobel, M.E. 1982. Asymptotic confidence intervals for indirect effects in structural equation models. Sociological Methodology 13, 290-312.

Sohmer, H., Pratt, H. 1977. Identification and separation of acoustic frequency following responses (FFRs) in man. Electroencephalography and Clinical Neurophysiology 42, 493-500.

Strait, D.L., Parbery-Clark, A., Hittner, E., Kraus, N. 2012. Musical training during early childhood enhances the neural encoding of speech in noise. Brain and Language 123, 191-201.

Thornton, A.R.D. 1975. The use of post-auricular muscle responses. The Journal of Laryngology & Otology 89, 997-1010.

Tierney, A.T., Krizman, J., Kraus, N. 2015. Music training alters the course of adolescent auditory development. Proceedings of the National Academy of Sciences of the United States of America 112, 10062-10067.

Weiss, M.W., Bidelman, G.M. 2015. Listening to the brainstem: Musicianship enhances intelligibility of subcortical representations for speech. Journal of Neuroscience 35, 1687-1691.

White-Schwoch, T., Anderson, S., Krizman, J., Nicol, T., Kraus, N. 2019. Case studies in neuroscience: Subcortical origins of the frequency-following response. Journal of Neurophysiology 122, 844-848.

White-Schwoch, T., Woodruff Carr, K., Thompson, E.C., Anderson, S., Nicol, T., Bradlow, A.R., Zecker, S.G., Kraus, N. 2015. Auditory processing in noise: A preschool biomarker for literacy. PLOS Biology 13, e1002196.

Wong, P.C., Skoe, E., Russo, N.M., Dees, T., Kraus, N. 2007. Musical experience shapes human brainstem encoding of linguistic pitch patterns. Nature Neuroscience 10, 420-2.

Yoshie, N., Okudaira, T. 1969. Myogenic evoked potential responses to clicks in man. Acta Otolaryngol Suppl 252, 89-103.

Yuval-Greenberg, S., Tomer, O., Keren, A.S., Nelken, I., Deouell1, L.Y. 2008. Transient induced gamma-band response in eeg as a manifestation of miniature saccades. Neuron 58, 429-441.

Zhao, T.C., Kuhl, P.K. 2018. Linguistic effect on speech perception observed at the brainstem. Proceedings of the National Academy of Sciences of the United States of America 115, 8716-8721.