Age-related hearing loss alters real-time dynamics of auditory cortical-brainstem coding during speech perception

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Abstract

Realtime modulation of brainstem frequency-following responses (FFRs) by online changes in cortical arousal state via the corticofugal (top-down) pathway has been demonstrated previously in younger humans and is more prominent in the presence of background noise. FFRs during high cortical arousal states also have a stronger relationship with speech behaviors. Aging is associated with overexaggerated auditory responses, which might reflect degraded inhibitory processing within the peripheral and ascending pathways, or changes in attentional control regulation via descending auditory pathways. Here, we tested the hypothesis that online corticofugal interplay is impacted in age-related hearing loss. We measured EEG in older adults with normal-hearing (NH) and hearing-loss (HL) while they actively performed speech identification tasks in different noise backgrounds. We measured α power to index online arousal states during task engagement and separate speech-FFRs according to fluctuations in cortical activity. We found cortical α power was smaller in the HL than NH group. In NH listeners, α-FFRs modulation for clear speech also resembled that previously observed in noise among younger adults. Cortical-brainstem modulation was further diminished by noise and with HL in older adults. Lastly, neural decoding showed low-α FFRs were more predictive of behavioral measures and carried more stimulus-related information of speech in NH individuals. Our findings provide evidence that age-related hearing loss affects cortical-brainstem interplay in the auditory system. Aberrant modulation of brainstem speech processing exposes a new underlying mechanism for the listening difficulties faced by older adults when engaging in cocktail party-like conversations.

Significant Statement

Top-down (e.g., attention and arousal) effects on human brainstem responses have been controversial. Here, we show that cortical activity (indexed by EEG α-band amplitudes) is associated with trial-by-trial changes in brainstem speech representations measured via frequency-following responses. More critically, we show these cortical-subcortical interactions are particularly prominent during active speech listening tasks in normal-hearing older adults and differentially changed in older adults with hearing loss. Our study reveals cortical arousal state actively shapes brainstem speech representations and provide a potential new mechanism for older listeners' difficulties perceiving speech in cocktail party-like listening situations in the form of a miss-coordination between cortical and subcortical levels of auditory processing.

Introduction

Declines in auditory processing (Poth et al., 2001; Parthasarathy et al., 2010; Kortlang et al., 2016; Lai and Bartlett, 2018) and speech comprehension (Anderson et al., 2012) (Schneider et al., 2005; Peelle et al., 2010)—especially in the presence of background noise (Dubno, 1984; Takahashi and Bacon, 1992; Souza et al., 2007; Anderson et al., 2011; Song et al., 2011; Jin et al., 2014; Presacco et al., 2016; Vermeire et al., 2016)—are ubiquitous during aging and age-related hearing loss. Age-related declines in the sensory (auditory) system (Parthasarathy and Bartlett, 2011, 2012; Fostick et al., 2013; Parthasarathy et al., 2014, 2016; Lai and Bartlett, 2015, 2018; Lai et al., 2017)[e.g., age-related impairments in sound

source segregation (Alain et al., 1996; Alain and McDonald, 2007; Gallun and Best, 2020)], changes in cognitive function (Park et al., 2003), or a combination of both (Pichora-Fuller and Singh, 2006; Wayne and Johnsrude, 2015; Wingfield et al., 2016) could lead to listening and comprehension difficulties.

Speech-in-noise (SiN) processing can be affected by many factors, such as attention (Saiz-Alía et al., 2019; Price and Bidelman, 2021) and arousal state (Mai et al., 2019; Saderi et al., 2021). Evidence from EEG studies on emotion suggest that cortical α band (8-12 Hz) is a useful indicator of arousal state (Aftanas et al., 2002; Uusberg et al., 2013). Moreover, parieto-occipital α activity was shown to index cognitive processing, effortful listening (Wöstmann et al., 2015; McMahon et al., 2016; Dimitrijevic et al., 2017), the state of wakefulness (Pfurtscheller et al., 1996) and top-down processing (Henry et al., 2017). Alpha oscillatory activity has also been associated with adaptive, intentional, and top-down suppression of task-irrelevant information (Rihs et al., 2007; Jensen and Mazaheri, 2010; Händel et al., 2011; Klatt et al., 2020). Increased α oscillations have been shown to play universal inhibitory roles across sensory modalities (Klimesch et al., 2007; Weisz et al., 2007, 2011; Strauß et al., 2014) while decreased α oscillations facilitate sensory processing or neural firing (Haegens et al., 2011; Klatt et al., 2020). The mechanisms underlying α oscillations reported in these studies are mixed and could be due to treating α as a unitary measure rather than reflecting different underlying processes. Meanwhile, some previous studies found influences of age in brain α oscillations (Yordanova et al., 1998; Böttger et al., 2002). Decreases in α frequency (Chiang et al., 2011) and reduced spontaneous entrainment of resting-state α oscillations (Gaál et al., 2010) were observed in older adults. Studying α power during SiN perception in older adults may reveal the impacts of aging in top–down

attentional control that help facilitate processing of target vs. non-target sounds, thus providing insight concerning why cocktail party-like situations are more difficult in older listeners (Pichora-Fuller et al., 2017).

In normal-hearing young listeners during active SiN perception, we recently demonstrated speech-evoked brainstem frequency-following responses (FFRs) during low cortical α activity were smaller than FFRs during high α states. Low-α FFRs also correlated positively with behavioral response times (RTs) for speech detection and more accurately decoded the input speech stimuli as revealed by neural classifiers (Lai et al., 2022). Extending this approach here to address questions of auditory aging, we analyzed neuroelectric FFRs recorded during active speech perception in age-matched older adults with normal (NH) or mild hearing loss (HL). This allowed us to investigate the effects of age-related hearing loss on cortical α state and its modulation of brainstem speech processing in real-time. We aimed to determine the nature of auditory cortical-brainstem interplay in the older population, and more critically, whether such online corticofugal engagement during SiN listening is altered due to hearing loss, as suggested in prior work (Bidelman et al., 2019). The overall results reveal that brainstem speech-FFRs are dynamically modulated by fluctuations in cortical α state in normal-hearing listeners but this cortical-subcortical interplay declines in age-related hearing loss.

Materials and Methods

Participant criteria. Detailed information of participants, informed consent, and demographics are reported in our original report detailing age-related changes in brainstem

and cortical evoked potentials (Bidelman et al., 2019). New analyses reported herein examine online changes in FFRs as a function of simultaneous cortical state. All participants had no reported history of neurological or psychiatric illness. Participants were divided into normal (NH) and hearing-impaired (HL) groups based on their pure-tone audiometry hearing thresholds. NH listeners (n = 13) listeners had average thresholds (250-8000 Hz) better than 25 dB HL across both ears whereas HL listeners (n = 19) had average thresholds poorer than 25 dB HL. The pure-tone averages (PTAs) (i.e., mean of 500, 1000, 2000 Hz) of NH listeners were ~10 dB better than in HL listeners (mean ± SD; NH: 15.3 ± 3.27 dB HL, HL: 26.4 ± 7.1 dB HL; $t_{2.71}$ = -5.95, $p < 0.0001$; NH range = 8.3-20.83 dB HL, HL range = 15.8-45 dB HL). Both NH (t_{12} = 0.15, p = 0.89) and HL (t_{18} = -2.02, p = 0.06) groups had symmetric PTA between ears. We were able to match NH and HL listeners based on other demographic variables while maintaining adequate sample sizes per group. Both NH and HL groups had elevated hearing thresholds at very high frequencies (≥ 8000 Hz), which is a typical sign of age-related presbycusis in older adults. Besides hearing, the two groups were matched in age (NH: 66.2 ± 6.1 years, HL: 70.4 ± 4.9 years; $t_{2.22}$ =-2.05, p = 0.052) and gender balance (NH: 5/8 M/F; HL: 11/8; Fisher's exact test, p = 0.47). Their age and hearing loss were not correlated (Pearson's r = 0.29, p = 0.10).

QuickSiN test. The Quick Speech-in-Noise (QuickSiN) test was used to measure listeners' speech reception thresholds in noise (Killion et al., 2004). A list of six sentences with five keywords per sentence spoken by a female talker in a background of four-talker babble noise were heard by listeners during the test. Target sentences were presented at 70 dB sound pressure level (SPL) (binaurally) at signal-to-noise ratios (SNRs) decreasing from

25 dB (relatively easy) to 0 dB (relatively difficult) in 5 dB steps. Number of keywords correctly recalled by listeners were logged and a score was computed for each listener. The SNR-loss score indexes the difference between a listener's SNR-50 (i.e., the SNR required to correctly identify 50 % of the keywords) and the average SNR threshold for normal-hearing adults (i.e., 2 dB) (Killion et al., 2004). A higher score reflects poorer SiN perception. Each listener's SNR-loss score was averaged from four lists of sentence presentations. In this study, NH listeners' scores ranged from -0.25 to 2.5 dB of SNR-loss (M = 1.1, SD = 0.8) while HL listeners' scores ranged from -2.5 to 8.5 of SNR-loss (M = 2, SD= 2.5) (see Fig. 1D in Bidelman et al., 2019).

Stimuli and task. The stimuli and task are described fully in Bidelman et al. (2019) and illustrated in Fig. 1A. Three naturally produced English consonant-vowel phonemes (/ba/, /pa/ and /ta/), from the standardized UCLA version of the Nonsense Syllable Test (Dubno and Schaefer, 1992), were generated by a female talker. The duration of each phoneme was 100-ms and the average root mean square SPL of each phoneme matched. All three tokens had a common voice fundamental frequency (mean F0 = 150 Hz), first and second formants (F1 = 885, F2 = 1389 Hz). The resulting stimulus-evoked response (i.e., FFR) should predominantly originate from the subcortex (Brugge et al., 2009; Bidelman, 2018) since the stimulus F0 is above the phase-locking limit of the cortical neurons and "cortical FFRs" (Coffey et al., 2016; Bidelman, 2018; Bidelman and Momtaz, 2021). Speech tokens were delivered binaurally to listeners in either clear (i.e., no noise) or noise-degraded conditions. A complete set of stimulus presentation in each condition contained a total of 3000 /ba/, 3000 /pa/, and 210 /ta/tokens (spread evenly over 3 blocks to allow for breaks). The

interstimulus interval between tokens was randomly jittered within the range of 95-155 ms (5ms steps, uniform distribution). The /ba/ and /pa/ tokens were presented more frequently than the /ta/ token in a pseudo-random manner such that at least two frequent tokens intervened between infrequent tokens. The infrequent /ta/ token was denoted as the target in which listeners were required to provide a response by pressing a button on the computer whenever they detected it. Both reaction time (RT) and detection accuracy (%) were recorded. For the noise-degraded condition, the same procedures as the clear condition were repeated but the tokens were presented in an identical speech triplet mixed with eight talker noise babble (Killion et al., 2004) at a signal-to-noise ratio (SNR) of 10 dB. There were 6 blocks (3 clear & 3 noise) collected from each participant. Having the clear and noise conditions allowed us to compare behavioral performance in different backgrounds and evaluate the impact of noise in speech perception in NH vs. HL listeners, respectively. The task ensured listeners to be actively engaged during speech perception and online EEG recording. Stimuli were controlled by MATLAB (The Mathworks, Inc.; Natick, MA) routed to a TDT RP2 interface (Tucker-Davis Technologies; Alachua, FL) and delivered binaurally through insert earphones (ER-3; Etymotic Research; Elk Grove Village, IL). The speech stimuli were presented at 75 dB SPL (noise at 65 dB SPL) with alternating polarity.

EEG recording & preprocessing. Neuroelectric activity was recorded from 32 channels at standard 10-20 electrode locations on the scalp (Oostenveld and Praamstra, 2001) during the target speech detection task. Electrode impedances were ≤ 5 kΩ. EEGs were digitized at 20 kHz using SynAmps RT amplifiers (Compumedics Neuroscan; Charlotte, NC). After EEG acquisition, the data were processed using Python 3.9.7. EEG data were re-referenced off-

line to the mastoids (TP9/10) for sensor (channel-level) analyses. For source analysis of brainstem FFRs, we used a common average reference prior to source transformation (detailed below). Responses were then filtered 100-1000 Hz [finite impulse response (FIR) filters; hamming window with 0.02 dB passband ripple, 53 dB stopband attenuation, -6 dB cutoff frequency] to further isolate brainstem activity (Musacchia et al., 2008; Bidelman et al., 2013).

Derivation of source FFRs & cortical activities. The derivation of source FFR waveforms and isolation of cortical activities are similar to the methods described in Lai et al. (2022). The 32-ch sensor data were transformed into source space using a virtual source montage. The source montage comprised of a single regional dipole (i.e., current flow in x, y, z planes) positioned in the brainstem and midbrain (i.e., inferior colliculus) [details refer to (Bidelman, 2018; Bidelman and Momtaz, 2021; Price and Bidelman, 2021)]. Source current waveforms (SWF) from the brainstem dipole were obtained using the formula: $SWF = L^{-1} \times FFR$, where L is the brainstem dipole leadfield matrix and FFR is the 32-ch sensor data. This applied an optimized spatial filter to all electrodes that calculated their weighted contribution to the scalp-recorded FFRs in order to estimate source activity within the midbrain (Scherg and Ebersole, 1994; Scherg et al., 2002). This model explains >90 % of the scalp-recorded FFR (Bidelman et al., 2019; Price and Bidelman, 2021). Only the z-oriented source activity was used in this study given the predominantly vertical orientation of current flow in the auditory midbrain pathways relative to the scalp [x- and y-orientations contribute little to the FFR (Bidelman, 2018)].

We isolated cortical α band activity from the EEG and used it as a running index of arousal state (high or low) during the target speech detection task. EEG at the Pz and Oz channels were filtered at 8-12 Hz (FIR filters) and averaged (i.e., equivalent to POz) to obtain cortical α-band activity at a posterior scalp region. Filtered α activities were epoched with a time window of 195 ms (-50 to 145 ms in which 0 ms corresponded to the onset of a /ba/ or /pa/ token) to capture approximately 1-2 cycles of α band. This epoch window encapsulated the entirety of the evoked FFR within the immediate trial with no spillover from the preceding or subsequent trial(s). Infrequent /ta/ tokens were excluded from analysis due to their limited trials. The root mean square (RMS) amplitude of single trial α activity was computed to quantify cortical arousal level over the duration of the target speech detection task. We then normalized RMS values to the median of RMS values of each run, respectively. Next, the distribution of trial-wise normalized α RMS was visualized using a histogram. We categorized trials falling within the 0-35th percentile as "low α" power and those falling within the 65-100th percentile as "high α" power. This categorization resulted in ~2100 trials for each low or high α power in each condition. More detailed information of this methodology can be found in Lai et al. (2022) (see their Fig. 2). We similarly measured cortical activity in another frequency band (e.g., β band; 18-22 Hz) from the same location (i.e., Poz β) and α band from a different electrode site (i.e., Fz α) as negative control analyses, i.e., to test whether FFR modulation was specific to α activity.

Analysis of brainstem FFRs. We categorized source FFRs based on whether α amplitude in the same epoch was either high or low power, thus deriving FFRs according to the trial-by-trial cortical state. Source FFR waveforms (from the z-orientated dipole) were

averaged for each α category and noise condition per participant. Subsequently, we analyzed the steady-state portion (10–100 ms) of FFR waveforms using the FFT (Blackman window; 11.1 Hz frequency resolution) to capture the spectral composition of the response. F0 amplitude was measured as the peak spectral maximum within an 11 Hz bin centered around 150 Hz (i.e., F0 of the stimuli). To compare FFR F0 amplitudes during low vs. high α power, a normalize (within-subject) F0 ratio was calculated as follows:

$$\text{F0 ratio} = \text{F0amp}_{\text{high}\alpha} / \text{F0amp}_{\text{low}\alpha} \quad (1)$$

Where F0 ratios > 1 indicate stronger brainstem FFRs during states of high cortical α power and F0 ratios < 1 indicate stronger FFRs during states of low cortical α power.

Stimulus-to-response cross-correlation. As the FFR waveform mimics periodic characteristics of the input stimulus, we examined the stimulus-relevant information carried by FFR waveforms during low or high arousal state. To this end, we computed cross-correlations between the acoustic stimuli (i.e., /ba/ and /pa/, clear condition) and their evoked FFR response. Token stimuli were first resampled to match the sampling rate of FFRs. Low- or high-indexed FFRs were further separated into /ba/- or/pa/-evoked FFRs. Subsequently, we performed cross-correlations between these FFRs and their eliciting stimulus and for the NH and HL groups. Stimulus-to-response cross-correlations were calculated by sliding FFR waveforms over the stimulus waveform on a point-by-point basis (Galbraith and Brown, 1990; Krishnan et al., 2005; Skoe and Kraus, 2010). As responses generated by the brainstem are expected to have a delay of at least ~10 ms (Tichko and Skoe,

2017; Bidelman, 2018), we focused our analysis within 10-20 ms after token onset and extracted the largest correlation at that time window for each token type, α power and NH or HL subjects. To test significance of the correlations, we time-shuffled the samples of the FFRs and repeated the same cross-correlation analysis to obtain a null destitution for the metric (i.e., hereafter called 'shuffled' correlations). A paired t-test was used to compare 'true' vs. 'shuffled' correlations. Moreover, we repeated the same procedures to compute miscorrelations of /ba/-evoked FFRs to /pa/ waveform and vice versa. This helped us to compare 'true' correlations with miscorrelations to better interpret token discriminability in FFRs during low vs. high α power (i.e., high vs. low arousal trials).

Experimental design and statistical analysis. A total of 32 older adults (F:16; M:16) aged 52-75 years were recruited from the Greater Toronto Area. Participants were assigned to NH and HL groups based on their hearing thresholds at octave frequencies between 250 and 8000 Hz. Participants of each group undergo EEG recordings while performing target speech (i.e., /ta/) identification task in a background of quiet (i.e., clear) or noise. Subsequently, FFRs and cortical α band were extracted from 32-ch running EEG for each frequent speech tokens (i.e., /ba/ and /pa/) to analyze and compare the differences in modulation of speech encoding by cortical α power in NH vs. HL group.

For statistical analysis, we used rmANOVAs to compare brainstem F0 ratios among the clear vs. noise condition, and NH vs. HL group. Multiple pairwise comparisons (Mann-Whitney U test with Bonferonni corrections) between the NH and HL groups were performed using the 'pingouin' package in Python. One sample t-tests ('scipy' package in Python) were also used to evaluate whether FFR F0 ratios were significantly different from

1 (and thereby indicated the significance of α modulation). Wilcoxon signed-rank test was used when comparing raw F0 amplitudes at low vs. high α power within subject for each SNR condition and hearing group. To assess differences in raw F0 amplitudes (log-transformed) across factors for NH and HL groups, we first performed a 2 x 2 x 2 (SNR x α power x hearing group) mixed model (subjects = random factor) ANOVA ('lme4' package in Rstudio). Following a significant interaction, we then ran separate 2 x 2 (α power x SNR) mixed-model ANOVAs for the NH and HL groups, respectively. Initial diagnostics were performed using residual and Q-Q plots to assess heteroscedasticity and normality of data. F0 amplitudes were log-transformed to improve normality and homogeneity of variance assumptions. Effect sizes are reported as η_p^2. In the clear condition, to evaluate differences in stimulus-to-response correlations across factors, we again used a 2 x 2 x 2 (token x α power x hearing group) mixed model ANOVA and later a 2 x 2 (token x α band power) mixed model ANOVA for NH and HL groups, respectively. This allowed us to assess the interaction effects of token type x α power separately in NH and HL groups. To test the significance of neural measures (raw FFR F0 amplitudes) in predicting behavioral performance (i.e., QuickSiN, PTA, %-correct, and RTs), we fit multiple linear regression models as follows:

$$Y = \beta_1 X + \beta_2 (SNR) + \beta_3 (\alpha\ power) + \beta_0 \qquad (2)$$

Where Y is the dependent variable (i.e., QuickSiN, PTA, %-correct, or RTs), and X is the independent variable representing F0 amplitudes. *SNR* and *α power* were dummy variables. Meanwhile, β_0 is a constant and β_n (n = 1, 2, or 3) is the coefficient for the respective

independent variable. Subsequently, we assessed pairwise linear relations between neural and behavioral measures via Spearman's correlations ('scipy' package in Python).

Results

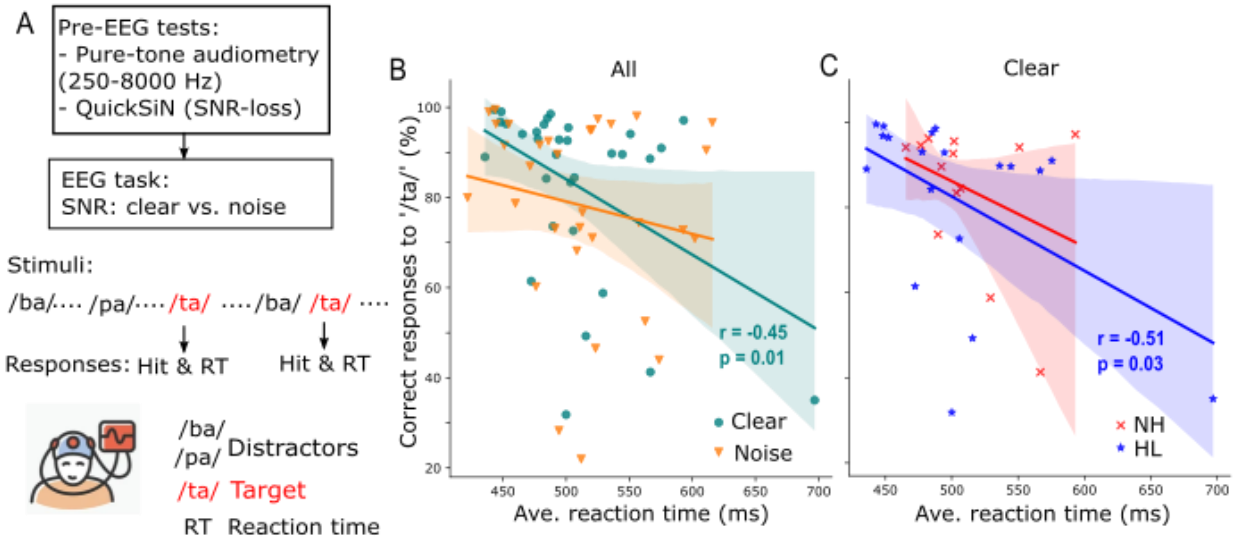

Figure 1. Target speech detection performance correlates with average response time collected during an active EEG task. (A) Prior to EEG recordings, all participants' pure-tone audiometry tested at 250-8000 Hz were obtained and speech-in-noise perception was assessed with QuickSiN. Subsequently, speech-EEGs to consonant-vowel phonemes (/ba/, /pa/ and /ta/) were recorded under clear or noisy (+10 dB SNR) backgrounds while participants actively engaged in the target speech detection task. (B) Correct responses to target speech (i.e., /ta/) are predictive of reaction times in quite (clear) but not noisy backgrounds. (C) When participants were divided into normal (NH) and hearing loss (HL) groups, the correlation of speech detection accuracy and reaction time obtained in quiet backgrounds is significant only in the HL group. r = Spearman's correlation; shaded area = 95 % CI of the regression line.

Behavior performance of target speech detection

Behavioral responses during the EEG task (%-correct /ta/ detections vs. RTs) showed a negative correlation for the clear but not noise condition (Spearman's r = -0.45, p = 0.01, Fig. 1B); participants with slower response speeds showed poorer speech detection accuracies.

This is consistent with previous findings showing negative associations between hit responses and RTs in younger listeners (e.g., Lai et al. 2022). When separated into the NH and HL groups, we found a negative relationship between behavioral hit responses and decision speeds but only in the HL group (Fig. 1C).

Cortical α band and brainstem speech-FFRs

Differences in cortical α-band amplitudes during low vs. high α states were prominent at the single participant (Fig. 2A) as well as group level (Fig. 2C). Spectral differences in the corresponding brainstem FFR for these same low vs. high cortical trials in the single participant were also notable, especially near the speech F0 frequency (150 Hz) (Fig. 2B). Cortical α was overall higher in the NH listeners ($p<0.01$, non-parametric post-hoc Conover's test with Bonferroni adjustment) but both groups showed clear separability of "low" vs. "high" α states during the rapid speech detection task.

In the clear condition (Fig. 2D), F0 ratios (indexing α-related FFR enhancement) in the NH group were significantly higher than 1 ($t_{12} = 2.64$, $p = 0.02$, 1-sample t-test) and higher than the HL group overall ($U = 192$, $p = 0.01$, Mann-Whitney U test). In the noise condition, this cortical-FFR enhancement was observed in the HL ($t_{18} = 2.67$, $p = 0.02$, 1-sample t-test), but was not significantly different than the FFR enhancement observed in the NH group. Repeating the same analytical procedures for both negative controls (POz β and Fz α) revealed no difference in F0 ratios for the NH vs. HL group, indicating cortical modulation of the FFR was restricted to the α frequency band.

A 3-way mixed-model ANOVA performed on log F0 amplitudes revealed a significant SNR x α power x group interaction ($F_{1, 96} = 9.5$, $p = 0.003$, $\eta_p^2 = 0.09$) (Fig. 2E). To make sense

of this complex interaction, we performed separate 2-way (SNR x α power) mixed-model ANOVAs by hearing group. The SNR x α power interaction was significant in both the NH ($F_{1,39} = 5.17$, $p = 0.03$, $\eta_p^2 = 0.12$) as well as the HL group ($F_{1,57} = 4.11$, $p = 0.05$, $\eta_p^2 = 0.07$). Though comparison of effect sizes suggests this interaction was stronger in NH listeners, the interaction was distinct in direction compared to the HL group. In the NH group, FFR F0 amplitudes were significantly higher during high α power for clear speech. This pattern was dampened and reversed in the HL group.

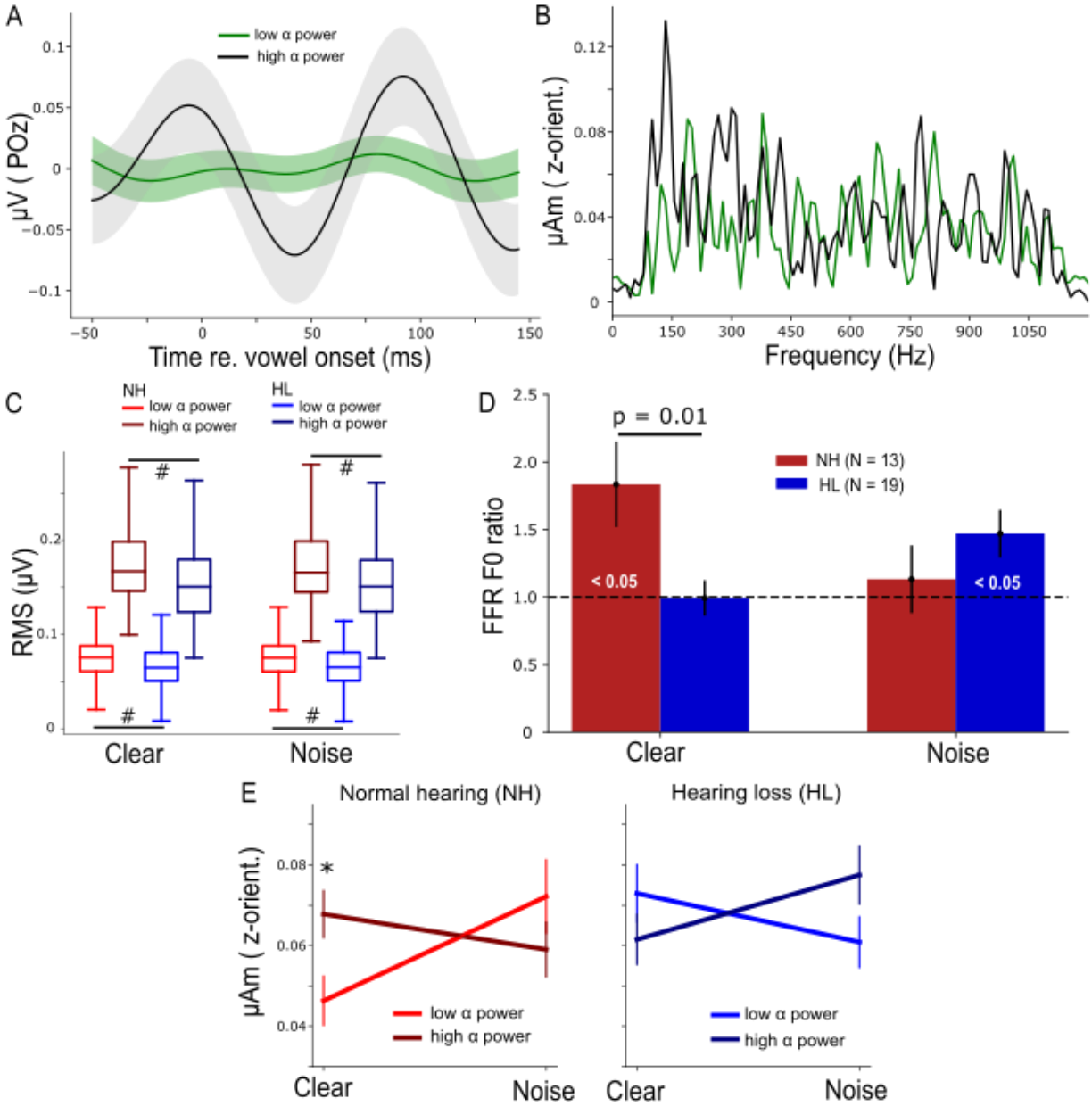

Figure 2. Normal hearing (NH) participants have a higher parieto-occipital α power and their brainstem speech processing is more strongly modulated by α band in clear backgrounds. (A) Average α waveform of low- and high-power trials plotted from a representative NH subject. (B) Frequency spectra of the steady state (10-100 ms) portion of low- and high-α brainstem FFRs from the same subject in (A). (C) Root-mean-square (RMS) values of both low and high α of the NH group were significantly higher than the HL group. # p< 0.01 (Conover's test, non-parametric pairwise test, with Bonferroni adjustment) (D) FFR F0 ratios during low and high α trials. FFR F0 ratios were higher in the NH vs. HL group (Mann-Whitney U test) in the clear condition. Bars marked (<0.05) are significantly larger than 1 (1-sample t-test). (E) Raw FFR F0 amplitudes as a function of SNR (clear vs. noise), α power (low vs. high), and group (NH vs. HL). Error bars= ± s.e.m., *p<0.05 (Wilcoxon signed-rank test).

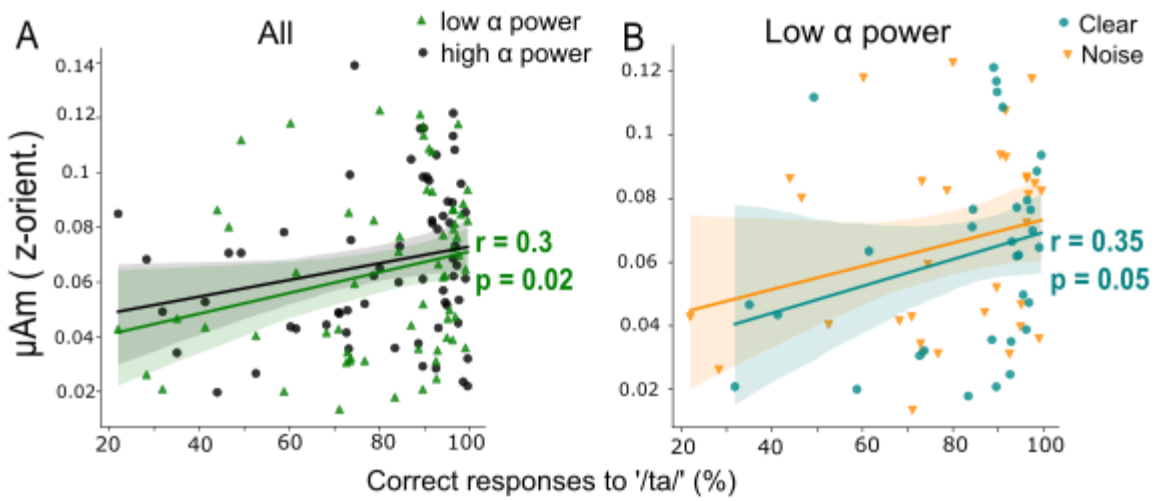

Figure 3. FFR F0 amplitude predicts behavioral speech perception during low cortical α power. (A) Low-α FFRs correlated positively with percent correct of speech target detection. (B) During low α, this positive brain-behavior association was significant only for clear speech. r = Spearman's correlation. Shaded area=95 % CI of the regression line.

Brain-behavior relations

We next assessed associations between neural measures (raw FFR F0 amplitudes) and behavioral performance (QuickSiN, PTA, %-correct, and RTs) by fitting multiple regression models (Eq. 2). When percent correct was used as the dependent variable (i.e., *Y*), the coefficient of F0 amplitude was significant ($\beta_1 = 1.7 \times 10^8$, t = 2.84, p = 0.005). This indicates that F0 amplitudes correlated positively with percent correction of /ta/ detections. When the correlation was analyzed separately for F0 amplitudes at low vs. high α power, the positive association between F0 amplitudes and percent correct remained significant at low but not high α power (Spearman's r = 0.3, p = 0.02, Fig. 3A). Furthermore, when restricting our analysis on low α power across SNRs, F0 amplitude predicted percent correct performance but only for clear speech (r = 0.35, p = 0.05, Fig. 3B). The same analysis conducted using POz β and Fz α were not significant. This again suggests the observed effects were specifically related to cortical α power and not general fluctuations in the EEG.

The aforementioned analyses showed that during high arousal states (i.e., with low α power), FFRs have a stronger relation with behavior compared to low arousal states (see Fig. 3A). Hence, we tested correlations of low-α FFRs with behavioral performance systematically and separately for the NH and HL groups. In both the clear and noise conditions, we found a significant negative association between F0 amplitudes at low α power and PTAs in the NH group (r = -0.42, p = 0.03, Fig. 4A). This indicates that NH participants with poorer PTAs have smaller low-α-indexed FFRs. When separating the data by SNR, the negative correlation was isolated to the HL group for clear speech (r = -0.53, p = 0.02, Fig. 4B). For noisy speech, we similarly found that PTA negatively predicted FFR strength but only for the NH group (r = -0.55, p = 0.05, Fig. 4C).

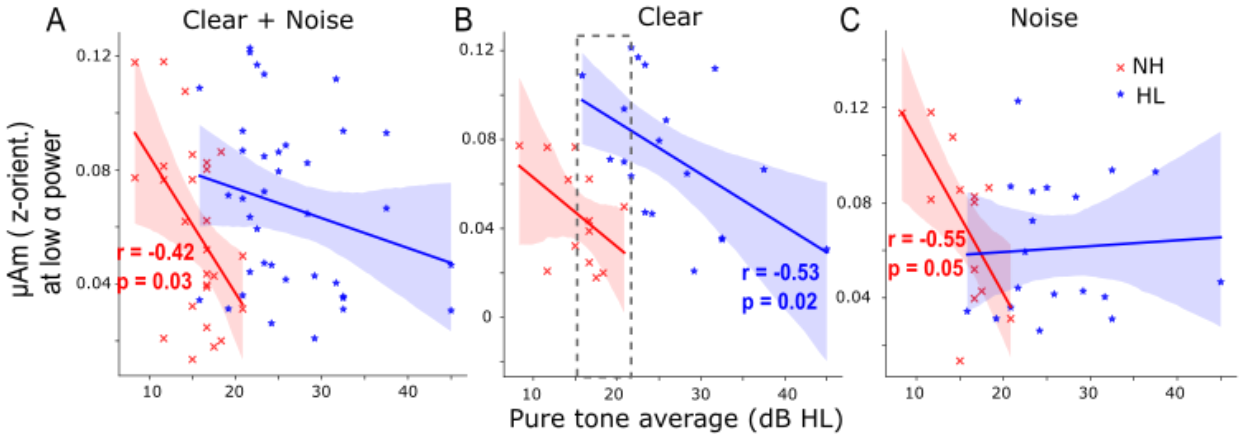

Figure 4. Hearing loss is associated with smaller speech-FFR amplitude under low cortical α states. (A) FFR F0 amplitudes during low α power negatively associated with PTAs in the NH group when pooling SNRs. (B) For clear speech, FFRs are weaker in older adults with more hearing loss. The gray dashed box marks the overlapping PTA region for both the NH and HL groups. (C) For noise-degraded speech, FFRs are associated with minimal hearing loss in the NH (but not HL) group. r = Spearman's correlation. Shaded area=95 % CI of the regression line.

Stimulus-to-response cross correlations

FFRs during low α power showed closer correspondence with behavior (Fig. 3) and PTAs (Fig. 4), suggesting brainstem speech representations during high cortical arousal states might better reflect the underlying speech acoustic signal. We formally tested this via stimulus-to-response cross-correlations between FFRs and their evoking stimulus waveforms. (Fig. 5). All but one value was significantly above the null distribution indicating stimulus-to-response correlations were above chance level. In general, /ba/-evoked FFRs showed closer correspondence with the stimulus waveform than /pa/ responses indicating an across-the-board stimulus effect (i.e., better encoding of /ba/). However, this stimulus contrast was observed under low α power for the NH group but high α power for the HL group.

A 3-way mixed-model ANOVA on stimulus-to-response correlations revealed a significant main effect of token ($F_{1,96} = 11.3$, $p = 0.001$, $\eta_p^2 = 0.11$) and interaction effect of token type x α power x hearing group ($F_{1,96} = 8.0$, $p = 0.006$, $\eta_p^2 = 0.08$). We then performed a follow up 2-way mixed-model ANOVA separately per hearing group. In the NH group, only the main effect of token type was observed ($F_{1,52} = 6.0$, $p = 0.02$, $\eta_p^2 = 0.1$). In the HL group, the token main effect ($F_{1,57} = 5.6$, $p = 0.02$, $\eta_p^2 = 0.09$) and the token type x α power ($F_{1,57} = 6.6$, $p = 0.01$, $\eta_p^2 = 0.10$) were significant. On the other hand, when we repeated the same analytical procedures on the miscorrelations (/pa/-evoked FFRs correlated to /ba/ waveform and vice versa), the ANOVA showed no significance.

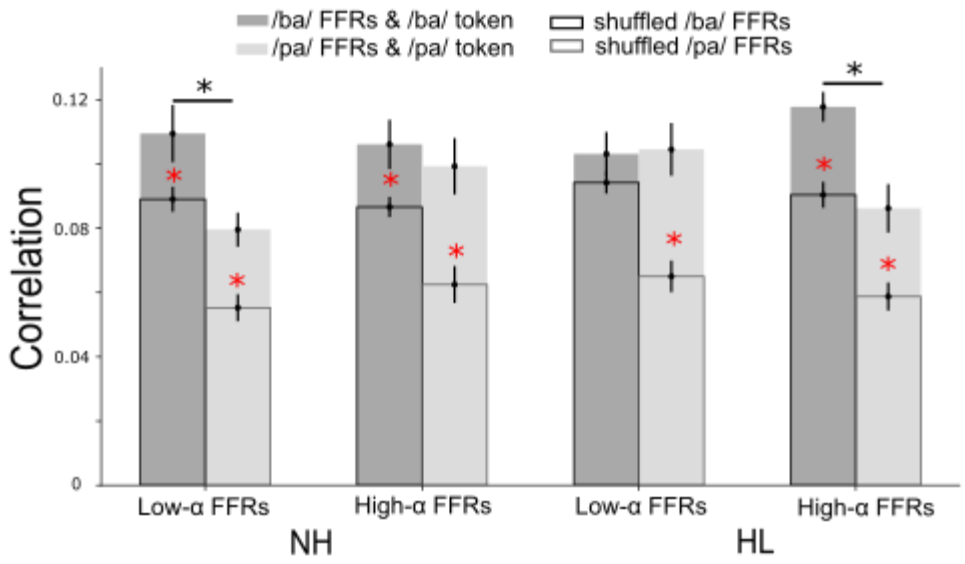

Figure 5. Distinct interaction effect of token x α power in brainstem speech-FFRs between older adults with and without hearing loss. FFRs evoked by /ba/ were cross-correlated to /ba/ waveform and vice versa. Larger differences in correlations when compared across /ba/ and /pa/ tokens at low α power were observed in the NH group, but larger differences in correlations at high α power were observed in the HL group. Red asterisks within bars indicated stimulus-to-response correlations were above chance level. Errorbars= ± s.e.m., * $p < 0.05$.

Discussion

Previous neuroimaging work reveals that functional connectivity between brainstem and cortex is weaker in older listeners with mild hearing loss and this interplay robustly predicts older adults' SiN perceptual performance (Bidelman et al., 2019). Adding to these findings, we show in NH older listeners, the existence of active and dynamic modulation of brainstem speech processing dependent on online changes in listeners' cortical state. This active and dynamic cortical-brainstem modulation, however, is diminished when processing speech in noise and in older adults with HL. Compared to NH listeners, HL listeners showed weaker parieto-occipital α power but those with minimal hearing loss (i.e., smaller PTA) had

unusually large FFRs during low α states (gray dashed box in Fig. 4B). Although FFRs were smaller during low α power, they were predictive of perceptual speech measures (Fig. 3) and differentially correlated with stimulus waveforms in the NH group (Fig. 5). Collectively, our findings suggest that (i) FFRs during low α power (i.e., high cortical arousal states) are more predictive of behavioral performance, and (ii) degraded corticofugal modulation of brainstem speech processing but increased central gain in older adults with hearing loss.

Effects of age on cortical α power and cortical modulation of brainstem speech processing

Cortical α indexes states of wakefulness and arousal (Pfurtscheller et al., 1996; Aftanas et al., 2002; Uusberg et al., 2013). Still, there is also evidence showing that α power may vary or index mind wandering during cognitive tasks (Compton et al., 2019; Maillet et al., 2020). Calculating the span length of low- or high-α trials for each listener showed averages of ~ 1.7 trials in both hearing groups, equating to several hundred milliseconds during our task. The relative speed of these fluctuations suggests that the α-modulations observed here are unlikely related to mind wandering *per se*, which presumably develops over longer time courses [tens of seconds (Pelagatti et al., 2020)]. Instead, we infer low α power tracks high arousal state while high α power reflects task focus but in a state of wakeful relaxation. Induced α activity is crucial for SiN perception as it might suppresses irrelevant information like noise to aid target speech processing (Strauß et al., 2014). In our previous study conducted in younger listeners (18-35 years) using similar EEG tasks, we observed larger α power to noise-degraded compared to clear speech during active engagement (see Fig. 2F in Lai et al., 2022). However, here in both NH and HL older adults, we do not find this same noise-related α effect. In general, α power was larger in NH than HL listeners (Fig. 2C).

Furthermore, high-α RMS values in older adults ranged from 0.1 to 0.4 μV whereas those in young listeners ranged from 0.1 to 1.0 μV. Therefore, we deduce that attenuated α power with no α enhancement in noise is related to aging itself. The observation of reduced α power with aging coincides with several studies (Babiloni et al., 2006; Purdon et al., 2015) and decreased α activity is also related to declines in cognitive functions with increasing age (Klimesch, 1997, 1999).

More critically, we demonstrate the presence of dynamic and online modulation of brainstem speech encoding by fluctuations in cortical α state in older NH adults that are fundamentally different than those observed in younger, normal-hearing listeners (Lai et al., 2022). In younger listeners, lower cortical α states positively correlate with smaller FFRs during speech perception against noisy backgrounds (Lai et al., 2022). Furthermore, low-α-indexed FFRs recorded in noisy backgrounds are predictive of behavioral RTs for rapid speech detection and have higher accuracies in token classification (Lai et al., 2022). Here, unlike younger listeners which require more difficult perceptual tasks (i.e., SiN perception) to tax the system and reveal effects of cortical arousal state on brainstem FFRs, we observed cortical modulation of FFRs in NH older adults during the perception of *clear* speech (Fig. 2D & E). Moreover, low-α-indexed FFRs associated with behavior [speech detection (Fig. 3) and PTAs (Figs 4)] and exhibited larger differences in stimulus-to-response correlations in the clear condition among the NH group (Fig. 5). Contrastively, in noise, low-α FFR amplitudes were not different from high-α FFRs and did not associate with any metric of perceptual performance. Taken together, the pattern of cortical-brainstem interactions in speech processing we found here in older NH listeners appears similar to what is found in younger listeners under challenging listening environments (cf. Lai et al, 2022). This indicates that

aging might alter cross-talk between functional levels of the auditory system under challenging listening conditions as a means of compensatory processing. Similar maladaptive plasticity has been previously observed at higher cortical levels where frontal brain regions are more strongly engaged to aid auditory-sensory coding in superior temporal gyrus (Price et al., 2019). This further suggests the presence of age-related deficits in top-down modulation of brainstem speech processing by cortex and provides an explanation to why older listeners find it more exhausting to participate in cocktail party-like listening situations compared to younger listeners (Pichora-Fuller et al., 2017).

Effects of hearing loss on cortical α power and cortical modulation of brainstem speech processing

Compared to the NH group, we observed decreases in parieto-occipital α power in the HL group in both SNR conditions (Fig. 2C). Lower α power is reported in listeners with moderate hearing-loss across the age spectrum (Petersen et al., 2015). Moreover, PTA correlates negatively with pre-stimulus α power in older listeners (Alhanbali et al., 2021). These findings are partly concordant with our data since we found lower α power (during stimuli) in older listeners with mild hearing loss. Furthermore, in the HL group, we found no cortical-related enhancements of FFRs (i.e., F0 ratio ≤1) for clear speech and responses were not different from the NH group in the noise condition though F0 ratio was > 1 (Fig. 2D). The interaction effect of SNR x α power was also distinct in direction between hearing groups. This finding implies that modulation of brainstem speech processing by cortical α state is altered in older listeners with mild hearing loss for both clear and noise-degraded speech processing.

In addition to parieto-occipital α power, PTAs was negatively correlated with low-α-indexed FFRs to clear speech in HL listeners (Fig. 4B) and noise-degraded speech for NH listeners (Fig 4C). A similar (though non-significant) trend was observed for NH responses to clear speech. The reduction in low-α FFRs with poorer PTAs is probably related to the decrease in peripheral hearing ability. However, when comparing across groups at comparable hearing loss (PTA = 15-22 dB HL), we found enhanced FFR amplitudes in HL listeners (gray dashed box in Fig. 4B). This suggests an increase in central gain probably related to high-frequency (> 4 KHz) hearing loss in the HL group (our NH listeners had normal audiometric thresholds up to 4 kHz). Similar central gain compensation secondary to peripheral hearing loss has been observed previously in both animal and human neuroimaging studies (Bidelman et al., 2014; Chambers et al., 2016). These phenomena were completely collapsed by noise in the HL group where low-α FFRs were relatively smaller in most HL listeners.

Stimulus-to-response cross-correlations revealed stronger differentiation of the speech signal in normal- vs. hearing-impaired FFRs. In the NH group, we observed a large difference in token-wise FFRs at low α power but no difference at high α power (Fig. 5). Contrastively, in the HL group, this pattern was inversed; /ba/ and /pa/ token FFRs were more discriminable during high α power. The result of the NH group was according to our expectation since low α indexes high arousal state and low-α FFRs correlated positively with behavioral speech detection accuracies (Fig. 3). Presumably, the more distinct neural representations we observe in FFRs during low cortical α states promotes improved speech discrimination. In younger listeners, we previously showed that neural decoding applied to low-α FFRs offered higher accuracies in token classification as compared to high-α FFRs (see

Fig. 5 in Lai et al., 2022). Thus, better speech token discrimination is consistently observed in FFRs during high arousal states in both normal-hearing younger and older adults. Although larger correlation differences were found in high-α FFRs in the HL group, they were not associated with perceptual performance. The mechanism underlying this observation in the HL group is unclear, but we speculate that this could be related to compensatory processing due to hearing loss.

Summary/Conclusion

Collectively, our study reveals age-related hearing loss not only reduces cortical α power but differentially alters its dynamic relationship with the subcortical speech processing. While brainstem speech processing is actively modulated by cortical arousal state in normal-hearing older adults, this modulation is disrupted by signal degradations (i.e., noise) and hearing loss. Speech-FFRs during low α states also offer a higher fidelity representation of the acoustic speech signature and are more predictive of perception than FFRs yoked to states of high cortical α. Enhanced FFRs in older adults with near-normal hearing (i.e., very mild hearing loss) suggest the presence of increased central gain compensation for reduced auditory input (Bidelman et al., 2014; Chambers et al., 2016).

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