Auditory-frontal Channeling in α and β Bands is Altered by Age-related Hearing Loss and Relates to Speech Perception in Noise

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Abstract—**Difficulty understanding speech-in-noise (SIN) is a pervasive problem faced by older adults particularly those with hearing loss. Previous studies have identified structural and functional changes in the brain that contribute to older adults' speech perception difficulties. Yet, many of these studies use neuroimaging techniques that evaluate only gross activation in isolated brain regions. Neural oscillations may provide further insight into the processes underlying SIN perception as well as the interaction between auditory cortex and prefrontal linguistic brain regions that mediate complex behaviors. We examined frequency-specific neural oscillations and functional connectivity of the EEG in older adults with and without hearing loss during an active SIN perception task. Brain-behavior correlations revealed listeners who were more resistant to the detrimental effects of noise also demonstrated greater modulation of α phase coherence between clean and noise-degraded speech, suggesting α desynchronization reflects release from inhibition and more flexible allocation of neural resources. Additionally, we found top-down β connectivity between prefrontal and auditory cortices strengthened with poorer hearing thresholds despite minimal behavioral differences. This is consistent with the proposal that linguistic brain areas may be recruited to compensate for impoverished auditory inputs through increased top-down predictions to assist SIN perception. Overall, these results emphasize the importance of top-down signaling in low-frequency brain rhythms that help compensate for hearing-related declines and facilitate efficient SIN processing. © 2019 IBRO. Published by Elsevier Ltd. All rights reserved.**

Key words: cognitive aging, EEG, functional connectivity, time–frequency analysis, neural oscillations, speech processing.

INTRODUCTION

Difficulty understanding speech-in-noise (SIN) is highly prevalent among the aging population including individuals both with and without hearing loss. Older adults exhibit greater listening effort (Anderson Gosselin and Gagné, 2011) and more significant performance deficits in adverse listening conditions than younger adults (Helfer and Wilber, 1990; Wong et al., 2010). Age-related hearing loss further exacerbates SIN difficulties (Helfer and Wilber, 1990). Previous studies characterizing the underlying mechanisms contributing to SIN difficulties reveal both peripheral and central brain mechanisms play a role in accurate and efficient SIN processing (Frisina and Frisina, 1997; Humes, 1996; Wong et al., 2010).

Indeed, neuroimaging studies reveal that structural and functional neural changes associated with aging (Bidelman et al., 2019a; Bidelman et al., 2019b; Du et al., 2016; Grady, 2012; Park and McDonough, 2013) contribute to older adults' SIN difficulties. Electrophysiological (EEG) studies often show exaggerated amplitudes and increased latencies of auditory cortical responses with aging, which has been taken as evidence for reduced inhibition (Alain and Woods, 1999; Bidelman et al., 2014; Caspary et al., 2008; Chao and Knight, 1997) and decreased temporal fidelity in the aging auditory system (Tremblay et al., 2003). The presence of hearing loss can amplify these changes due to the typical aging process (Lin et al., 2014; Pichora-Fuller and Levitt, 2012; Wayne and Johnsrude, 2015), resulting in even greater increases in response amplitude and latency when those with hearing loss are compared to their normal hearing peers (Alain et al., 2014; Campbell and Sharma, 2013; Cardin, 2016).

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To date, EEG studies have primarily relied on event-related potentials (ERPs) to infer the neural processes contributing to SIN perception. However, evaluating changes in gross activation within isolated brain regions can lead to misleading or ambiguous conclusions regarding the neurobiology of aging (Morcom and Henson, 2018; Wong et al., 2010). For instance, increases in evoked response amplitude commonly observed in older adults may be due either to the recruitment of additional neural resources (Bidelman et al., 2014; Wong et al., 2010), disinhibition (Bidelman et al., 2014; Caspary et al., 2008), or inefficient neural coding (Fabiani et al., 2006). Evaluating ERPs alone prevents full understanding of the underlying mechanisms of aging, particularly how different brain regions might coordinate to orchestrate successful SIN perception. Alternative EEG analyses may better delineate the underlying neural mechanisms for speech processing that are not always apparent with traditional ERP approaches (Bidelman, 2015; Bidelman, 2017; Yellamsetty and Bidelman, 2018).

In this vein, neural oscillations have provided novel insight into functional neural networks underlying complex perceptual and cognitive functions. Therefore, evaluating oscillatory components of neural responses may provide a more sensitive measure and more thorough understanding of the neural correlates of speech processing. Different brain "rhythms" are thought to play unique roles in the hierarchy of speech processing. High frequency γ oscillations are thought to contribute to localized processing within sensory cortices (Fontolan et al., 2014; Giraud and Poeppel, 2012; von Stein and Sarnthein, 2000) and the extraction of acoustic features (Yellamsetty and Bidelman, 2018) while lower frequency α and β oscillations have been involved in global, distributed cognitive processing across brain regions (Fontolan et al., 2014; von Stein and Sarnthein, 2000) including attention (Klimesch, 2012), inhibition of irrelevant cues (Adrian and Matthews, 1934; Klimesch, 2012; Pfurtscheller, 2001), working memory (Shahin et al., 2009; Zarahn et al., 2007), and template matching (Bidelman, 2015; Bidelman, 2017; Shahin et al., 2009; Yellamsetty and Bidelman, 2018). Evaluating how neural oscillations within different frequency bands of the EEG contribute to speech processing could provide further insight into the underlying processes supporting SIN perception in older adults.

In our ongoing studies on aging and the brain, we recently documented subtle neurophysiological changes in older adults with normal hearing (NH) and mild hearing loss (HL) that may reflect deficits in speech representations (Bidelman et al., 2019b). Using source-resolved brainstem and cortical ERPs, we found somewhat spared region-specific responses to speech, at least in listeners with mild hearing impairment. More significant differences were identified in functional connectivity between the auditory brainstem and cortex, suggesting neural transmission within the early auditory pathway is critical for robust SIN processing in older adults. Additional full-brain, functional connectivity analysis revealed more widespread and less efficient connectivity patterns in HL compared to NH listeners suggesting more diffuse

processing strategies are employed in those with hearing loss (Bidelman et al., 2019a). However, neither of these studies addressed the role of neural oscillations and how functionally distinct frequency channels of the EEG relate to senescent changes in SIN perception. Moreover, how the aging lemniscal hearing system (e.g., auditory cortex) interfaces with high-order brain regions that support linguistic decisions (e.g., prefrontal areas) is not well understood.

The current study aimed to examine contributions of neural oscillations and their role in neural signaling between auditory cortical and linguistic brain areas during SIN processing. In this reanalysis of our existing dataset (Bidelman et al., 2019b), we measured frequency-specific neural oscillations and functional connectivity via EEG in older adults with and without hearing loss during SIN perception tasks. Based on previous studies on aging, the effects of hearing loss on SIN processing, and putative roles of neural oscillations, we hypothesized that differences in α activity would emerge in more difficult listening conditions and that HL listeners would demonstrate enhanced connectivity between auditory and prefrontal cortex to compensate for poorer signal transmission apparent in earlier stages of the speech hierarchy (e.g., diminished brainstem-cortical connectivity; Bidelman et al., 2019b). Our findings reveal that (1) modulations in α phase coherence between clean and noise-degraded speech predicts accuracy in SIN tasks; (2) changes in functional brain connectivity occur without measurable behavioral deficits in SIN processing; (3) "top-down" β connectivity increases in strength with increasing severity of hearing loss suggesting that the transfer of information between auditory-linguistic brain regions may be more sensitive to hearing-related changes than localized activity within regions.

EXPERIMENTAL PROCEDURES

Analyses of the ERPs and behavioral responses associated with this dataset are reported in Bidelman et al. (2019b). New time–frequency analyses (applied here) were used to evaluate the correspondence between rhythmic brain oscillations and SIN perception in older adults.

Participants

Thirty-two older adults ranging in age from 52 to 75 years were divided into two groups based on their average hearing thresholds (Fig. 1A). Listeners with average thresholds better than 25 dB HL comprised the normal hearing (NH; $n = 13$) group while average thresholds worse than 25 dB HL classified participants with hearing loss (HL; $n = 19$). The level of 25 dB HL reflects the upper limit of the normal hearing range as specified by the clinical determination of hearing loss (Gelfand, 2009). The groups were otherwise matched for age (NH: 66.2 ± 6.1 years, HL: 70.4 ± 4.9 years; $t_{22.2} = -2.05$, $p = 0.052$) and gender (NH: 5/8 male/female; HL: 11/8; Fisher's exact test, $p = 0.47$) (for complete demographic details, see Bidelman et al., 2019b).
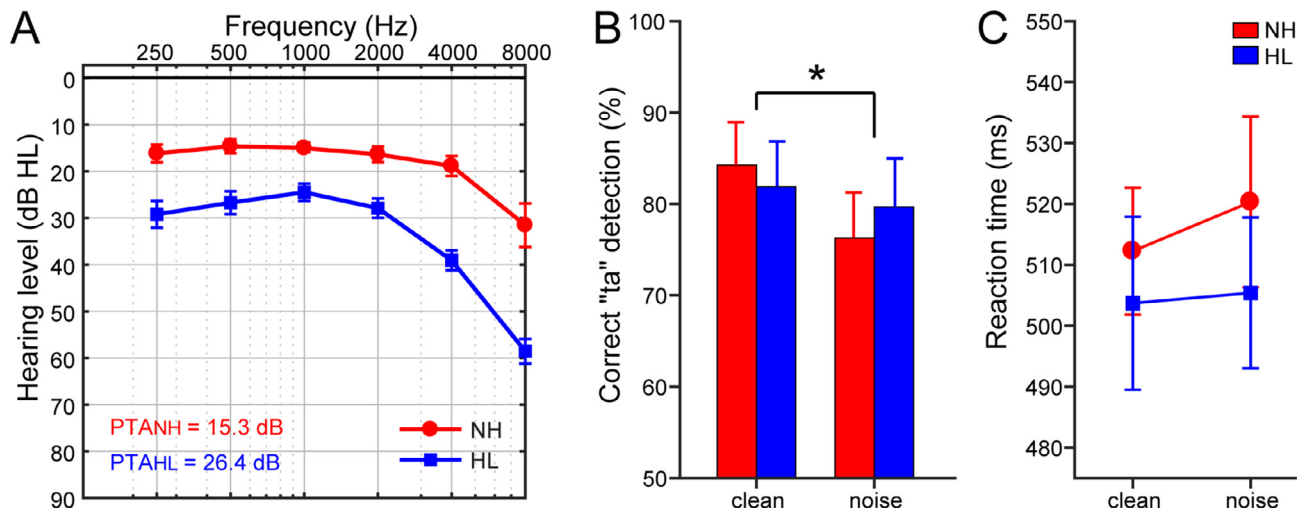
Fig. 1. Audiometric and behavioral results. Adapted from Bidelman et al. (2019b) with permission from Springer-Verlag. (A) Audiograms for listeners with normal hearing (NH) and hearing loss (HL). Hearing was ~10 dB better in NH vs. HL listeners. (B) Behavioral accuracy for detecting infrequent /ta/ tokens in clean and noise-degraded conditions. Noise-related declines in behavioral performance were prominent but no group differences were observed. (C) Reaction times (RTs) for speech detection were similar between groups and speech SNRs. Errorbars = ± s.e.m., *$p < 0.05$.

Stimuli and task

Electrophysiologic responses were recorded while participants performed an active SIN perception task in which they were directed to identify an infrequent speech token (i.e., /ta/) via button press. The stimuli included three naturally produced English consonant–vowel phonemes (/ba/, /pa/, and /ta/) spoken by a female talker. The stimuli were presented binaurally in clean (i.e., no background noise) and noise-degraded conditions [10 dB signal-to-noise ratio (SNR) using 8-talker babble noise, cf. Killion et al., 2004]. In each condition, the frequent tokens /ba/ and /pa/ were each presented 3000 times while the infrequent, target token /ta/ was presented 210 times. Between presentations, the interstimulus interval was randomly jittered between 55 and 155 ms (5 ms steps, uniform distribution). Both speech detection accuracy (%) and reaction times (RTs) were logged. See Bidelman et al. (2019b) for additional task details.

EEG time–frequency analysis on source waveforms

The EEG recording protocol and data pre-processing is described in our original report (Bidelman et al., 2019b). Briefly, cortical event-related potentials were recorded from 32 channels across the scalp. Ocular artifacts (saccades and blinks) were first corrected in the continuous EEG using a principal component analysis (PCA) (Picton et al., 2000). Cleaned EEGs were then epoched (−10–200 ms) and baseline corrected to the pre-stimulus period for each trial and stimulus condition per participant. The pre-stimulus interval was limited due to the interstimulus interval used during the perceptual task.[‡]

[‡] For the current study, the paradigm was designed to record frequency-following responses (FFRs) from the brainstem and cortical ERPs simultaneously. Because FFRs require many more trials (approximately 2000 per token) than traditional ERPs, shortening the interstimulus interval was necessary to reduce the overall time required for data collection.

To first reduce the dimensionality of the data and enable functional connectivity analysis between brain regions of interest (ROIs), full band (1–100 Hz), single trial scalp potentials were transformed to source space using the AEP virtual source montage in BESA (Scherg et al., 2002). This process applies a spatial filter to all electrodes and optimizes the relative weights of their contribution to the recorded scalp response to estimate the activity within each source while reducing overlapping activity from other brain regions (for details, see Scherg and Ebersole, 1994; Scherg et al., 2002). This allowed us to reduce each listener's EEG (32-channels) to 15 source channels with regional dipoles in bilateral primary auditory cortex (PAC), left/right frontal cortex near inferior frontal gyrus (IFG) (i.e., Broca's area), and left/right parietal cortex as well as sources along the mid-line (depicted in Fig. 1A of Zendel and Alain, 2014). From this model, we extracted the estimated neural current within single ROIs of the brain most relevant to our hypotheses including tangential and radial components of each auditory source, as these orientations capture the majority of the auditory cortical ERPs (Picton et al., 1999), as well as the radial components of each frontal source (BESA default). Furthermore, the selection of these sources enabled us to assess the effects of hearing loss on band-specific connectivity between auditory (PAC) and linguistic (IFG) brain areas and potential recruitment of additional neural resources (e.g., compensatory processing) due to age-related hearing loss. Time-frequency analysis (TFA) was then performed on the single-trial epochs at the source level to improve spatial accuracy and reduce smearing due to volume conduction (Hoechstetter et al., 2004) using BESA® Research v7 (BESA, GmbH).

TFA assessed the frequency-specific contributions of time-locked neural oscillations to older adults' SIN processing. Prior to TFA analysis, additional artifact correction was performed using a threshold of ± 120 μV. Initial analysis revealed negligible induced activity likely due to the restricted baseline (10 ms); therefore,

subsequent analyses focused on phase-locked oscillatory activity. The time–frequency transformation was achieved using a sliding window complex demodulation (for detailed description, see Papp and Ktonas, 1977) using 10 ms/5 Hz resolution step sizes. These settings permitted analysis of frequencies $\geq$10 Hz (i.e., α band and higher) across the entire epoch window. The resulting time–frequency displays, akin to neural spectrograms (see Fig. 2), were then produced by computing inter-trial phase-locking (ITPL) at each time–frequency point across single trials (Hoechstetter et al., 2004).

ITPL measures the phase consistency (i.e., trial-to-trial synchrony) of neural activity within each frequency band across time (Tallon-Baudry et al., 1996). Values range from 0 to 1 indicating the degree of phase synchronicity across trials (i.e., 0 – random noise; 1 – perfect trial-to-trial repeatability). For each ROI, we extracted band-specific time courses from the ITPL spectrograms in the α (10–12 Hz), β (15–29 Hz), low γ (30–59 Hz), and high γ (60–90 Hz) frequency bands (e.g., Bidelman, 2017) (see Fig. 3). We then measured the peak maximum ITPL and associated latency from each band waveform using MATLAB. Latency windows were guided by visual inspection of the grand averaged traces [α: 25–100 ms; β: 25–75 ms; low/high γ: 15–50 ms]. Peak responses were then used to assess the effects of SNR and hearing loss on neural oscillations involved in older adults' SIN perception.

Functional connectivity

We measured band-specific functional connectivity between PAC and IFG sources (for each hemisphere) using phase transfer entropy (PTE) (e.g., Bidelman et al., 2018; Bidelman et al., 2019b; Lobier et al., 2014). PTE is a directional measure of signal dependence. Additionally, PTE can be implemented in a frequency-specific manner to assess connectivity in individual EEG bands (Lobier et al., 2014). We computed PTE between source signals in the PAC and IFG ROIs in both directions (i.e., X → Y and Y → X) to quantify differences in the strength of afferent/bottom-up (PAC → IFG) vs. efferent/top-down (IFG → PAC) connectivity within the auditory-linguistic pathway as a function of speech SNR and group.

Statistical analysis

Mixed model ANOVAs were performed to assess all dependent variables of interest (GLIMMIX, SAS® 9.4, SAS Institute; Cary, NC) with participants serving as a random effect. Degrees of freedom were estimated using PROC GLIMMIX's containment option[§]. Unless otherwise specified, Bonferroni adjustments controlled for Type I error inflation. The significance level for all statistical analyses was set at α = 0.05. Independent samples t-tests (un-pooled variance, two-tailed) were

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[§] To satisfy model convergence and ensure estimable variance, it was necessary to remove the random term for the efferent (IFG-PAC) β connectivity variable. In this case, PROC GLIMMIX estimated degrees of freedom using the between-within approximation procedure (Schluchter & Elashoff, 1990), which divides the residual degrees of freedom into between-subject and within-subject portions.

used to compare demographic variables between groups. Correlational analyses (Pearson's-r) and robust regression (bisquare weighting - achieved using the 'fitlm' function in MATLAB) were used to evaluate relationships between neural and behavioral measures. Specifically, to evaluate the relationship between neural oscillations and behavioral SIN perception, we used robust regression. We first collapsed clean and noise responses by computing their difference (clean – noise). We then conducted correlational analyses between neural responses (i.e., phase coherence peak amplitude/latency within each frequency channel and source) and the behavioral measures [i.e., pure-tone average (PTA), RT, %]. This allowed us to assess the degree to which modulations in neural oscillations between clean and noise-degraded speech were related to changes in hearing thresholds and behavioral performance. False discovery rate (FDR) was used to correct for multiple correlations (Benjamini and Hochberg, 1995). One RT data point was identified as an outlier and was excluded from correlation analyses. All analyses and results were collapsed across the frequent tokens (i.e., /ba/ and /pa/) to further reduce the dimensionality of the data. Responses to infrequent /ta/ tokens were not included in analysis due to the limited number of trials and to avoid mismatch negativities.

RESULTS

Behavioral data

Behavioral responses, reproduced from Bidelman et al. (2019b), are shown in Fig. 1 and are reported in depth in that study. In short, we found no differences between groups in accuracy (Fig. 1B) nor RT (Fig. 1C) for target speech detection. However, noise had an expected detrimental effect on perceptual accuracy for both groups (Fig. 1B).

Electrophysiological data

Time-frequency (ITPL) spectrograms for the PAC and IFG sources are shown for each SNR and group in Fig. 2. Band time courses are shown in Fig. 3. Diagnostics for amplitude analyses revealed a positive skew; thus, a cube-root transform was used. ANOVAs conducted on the transformed amplitude measures revealed significant effects of SNR for all frequency bands (all $p < 0.03$) but no main effect of group or SNR × group interaction. For latency, no significant group or SNR effects were observed for any frequency band. The lack of group effects might be anticipated given the relatively mild differences in hearing loss between groups and our previous study, which did not observe differences in ERP responses (Bidelman et al., 2019b). This further motivates the examination of band-specific oscillations in these data.

To determine whether neural activity within different frequency bands was associated with perceptual SIN measures, we used robust regression to assess brain-behavior relations. We found a significant negative correlation between α oscillations in the right frontal
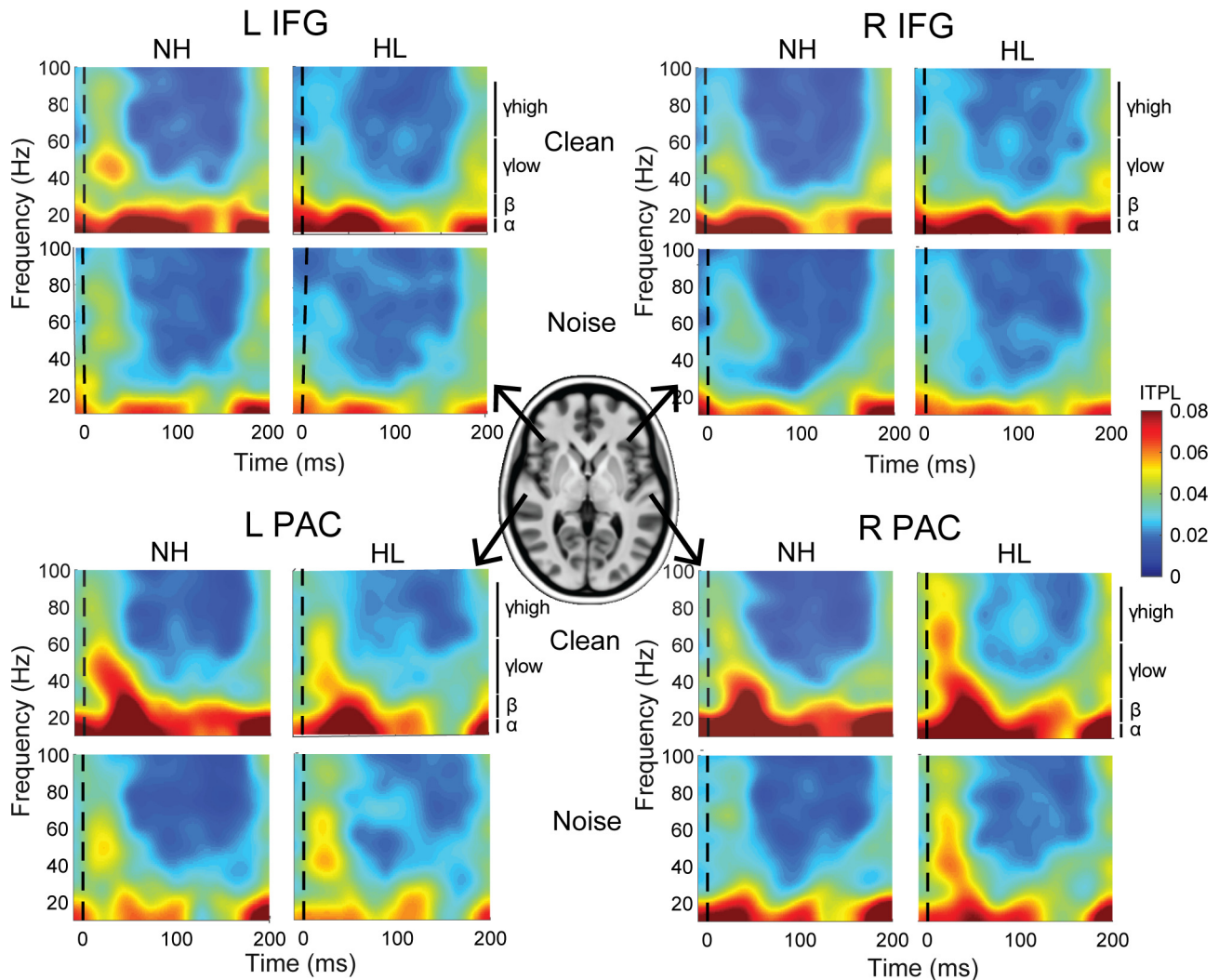
Fig. 2. ITPL spectrograms for radial auditory and frontal sources by SNR and group. Time-frequency analysis demonstrates phase synchrony (ITPL) within each neural source across frequency and time. Trending differences are observed when comparing synchronicity across sources (PAC > IFG), SNR (clean > noise), and group. Warm colors denote stronger neural phase synchrony across trials.

(IFG) source and speech detection accuracy [r_{30} = 0.41, p_{FDR} = 0.007; Fig. 4; left IFG: r_{30} = 0.02, p_{FDR} = 3.008; not shown]. This suggests that listeners who were more resistant to the detrimental effects of noise (i.e., performed equally as well or better in noise) also demonstrated less coherence of α activity while performing the SIN perception task. Little to no change in α phase coherence was observed in the listeners who performed more poorly in noise.

**Auditory-frontal functional connectivity**

We next asked whether differences in neural *transmission* (i.e., feedforward or feedback connectivity) between PAC and IFG is altered in individuals with mild hearing loss. Because initial inspection of the data revealed minimal connectivity within the low and high γ frequency bands (data not shown), subsequent analyses focused on connectivity within the α- and β-band channels. Mixed model ANOVAs (subjects = random effect) were performed for both afferent (PAC → IFG) and efferent (IFG → PAC) connectivity to evaluate the effects of group, hemisphere, and condition as well as potential interactions. These analyses were conducted separately by frequency band and each dipole orientation (i.e., tangential and radial). These analyses revealed that HL listeners demonstrated stronger *efferent* β connectivity between IFG and the radial PAC component than NH listeners (*mean ± SE*; HL: 0.28 ± 0.02, NH: 0.20 ± 0.02; $F_{1,30}$ = 7.14, p = 0.0121; Fig. 5A) regardless of SNR. In contrast, afferent (PAC → IFG) signaling did not differ between groups (HL: 0.27 ± 0.03, NH: 0.29 ± 0.03; $F_{1,30}$ = 0.08, p = 0.78; Fig. 5A). None of the other comparisons or interaction effects remained statistically significant following correction for multiple comparisons.

Lastly, to relate neural connectivity effects to behavior, we conducted correlations between β connectivity (the only band showing group differences) and behavioral measures (i.e., PTA, RT, %). As in the previous
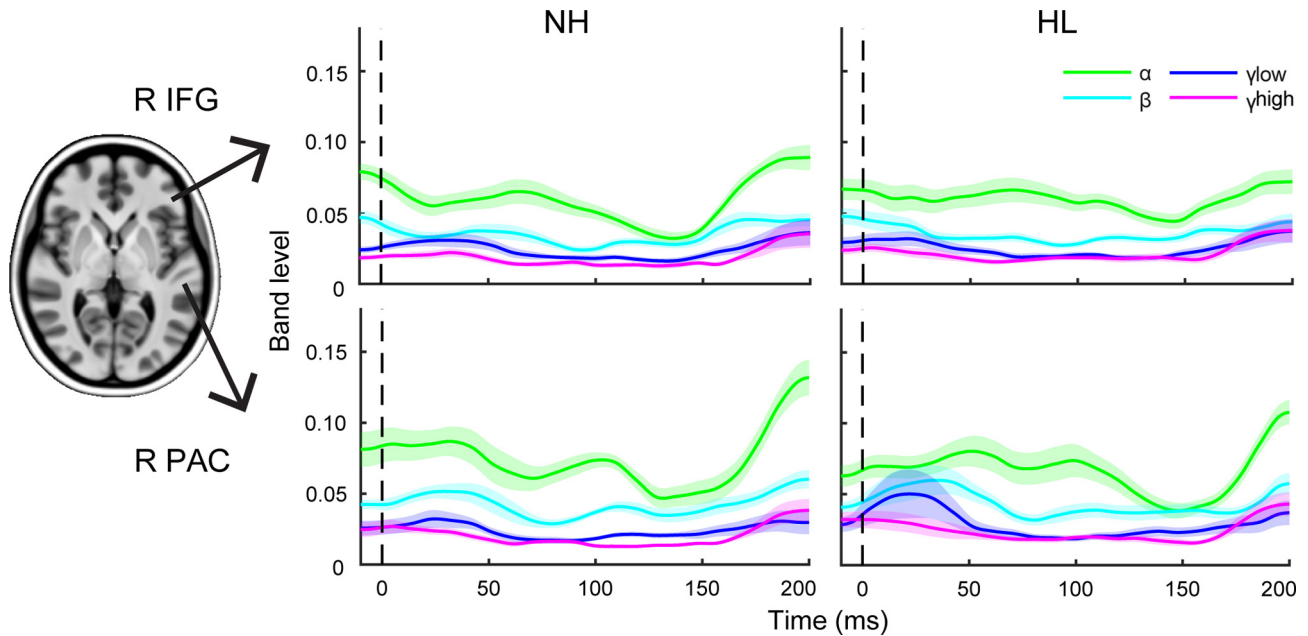
Fig. 3. Band-specific time-course waveforms within auditory and frontal sources. The time-course waveforms illustrate the degree of phase synchronicity across trials over time for each frequency band. Bands were extracted from ITPL maps (see Fig. 2). Waveforms reflect grand averaged traces for each group from the right frontal and auditory sources in the noise condition. Clean and left hemisphere responses not shown.
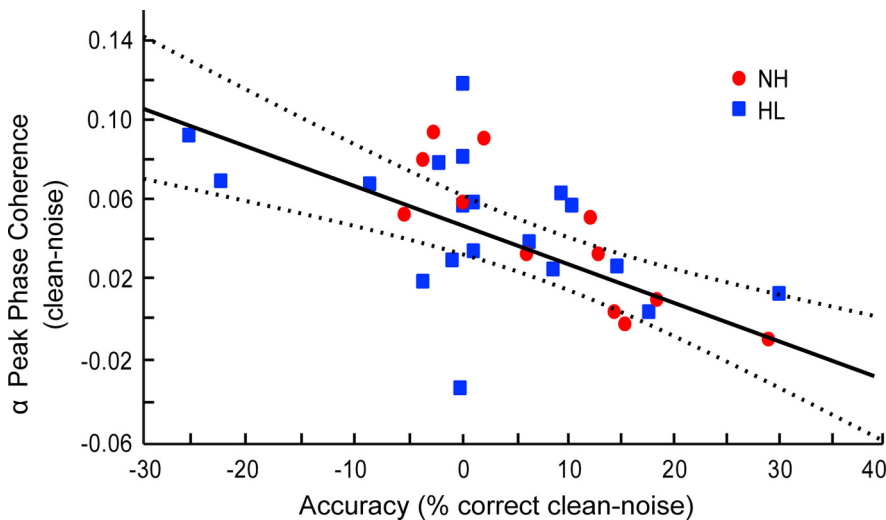
Fig. 4. Phase coherence within right IFG α-band predicts accuracy of SIN performance. Difference scores between clean and noise conditions are plotted for α phase coherence within right IFG and /ta/ detection accuracy for each participant. Greater modulations in α band are observed in listeners whose behavioral performance was more resistant to the detrimental effects of noise. Dotted lines represent the 95% confidence interval.

correlation analyses, we used difference measures between clean and noise responses in these calculations. We found that efferent β connectivity (in noise) between IFG and radial PAC was positively correlated with PTA ($r_{30} = 0.24$, $p = 0.0044$; Fig. 5B), such that stronger efferent connectivity was associated with greater degrees of hearing loss. No other significant correlations were noted including those involving the clean speech responses.

DISCUSSION

By measuring neural oscillations in older adults during SIN perception, our data reveal three primary findings: (1) modulations in α phase coherence between clean and noise-degraded speech predicts accuracy in SIN perception; (2) changes in functional brain connectivity precede measurable behavioral deficits in SIN processing; (3) "top-down" β connectivity from IFG to PAC increases in strength with increasing severity of hearing loss.

α phase coherence predicts accuracy in SIN perception

We found that older adults who were more resistant to the detrimental effects of noise behaviorally demonstrated reduced α phase synchronicity in noise, particularly within right IFG. Previous studies suggest that α enhancement functions to inhibit task-irrelevant inputs (Adrian and Matthews, 1934; Pfurtscheller, 2001) while reductions in α facilitate task-relevant processing (Klimesch, 2012). Similar to our findings, greater event-related desynchronization (ERD) in α has been related to improved performance in semantic (Doppelmayr et al., 2005; Klimesch et al., 1997) and working memory (Bashivan et al., 2014) tasks. Klimesch et al. (2007) further suggest that
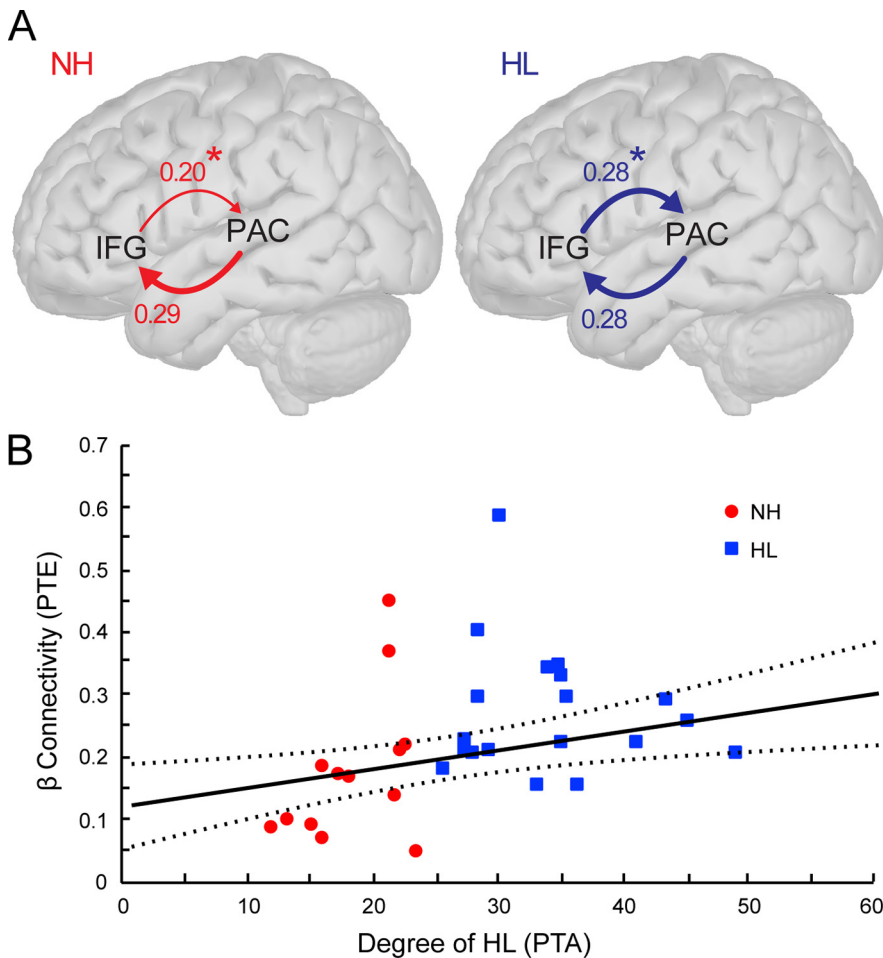
Fig. 5. Efferent functional connectivity (IFG → PAC) within β band varies with degree of hearing loss. (A) Phase transfer entropy reflecting the directed (casual) afferent (PAC → IFG) and efferent (IFG → PAC) neural signaling between auditory and prefrontal cortex for the noise degraded speech condition. Efferent connectivity is stronger in listeners with hearing loss compared to those with normal hearing; afferent connectivity is similar between groups. (B) Efferent IFG → PAC connectivity increases in strength in listeners with poorer hearing (i.e., higher PTAs). Dotted lines represent the 95% confidence interval. *$p < 0.05$.

ing more difficult noisy conditions, less synchrony within α band, reflecting a release from inhibition, may enable the brain to deploy attention more flexibly to aid syllable detection accuracy. While these outcomes are limited to phase-locked neural oscillations, changes in induced activity may reveal different underlying mechanisms of SIN processing (Bidelman, 2015; Petersen et al., 2015). Future studies could incorporate analyses of induced activity to provide a more thorough representation of event-related neural processes contributing to SIN tasks.

Paralleling our data, previous studies have also shown that age-related changes in α activity are localized to frontal and sensorimotor regions (Dushanova and Christov, 2016; Nobukawa et al., 2019). Activity within frontal cortical areas may serve as a compensatory mechanism for deficits in speech processing in older adults, particularly in more adverse listening conditions (Binder et al., 2004; Du et al., 2016; Zekveld et al., 2006). Specifically, IFG and superior temporal gyrus (STG) activation within the right hemisphere is particularly salient for difficult sound contrasts (cf. our noise condition) (Doeller et al., 2003). Furthermore, increased α activity within the right hemisphere, particularly IFG, has been associated with inhibitory processes (Garavan et al., 1999), which provides additional support to our conclusion that desynchronization in α activity within right IFG functions as a release from inhibition in older adults' speech-in-noise processing. Additional evidence of right lateralized compensation in SIN processing has been observed in passive listening tasks in normal hearing young adults, which reveals altered neural response laterality from being leftward dominant to include greater right hemispheric contribution within both PAC and IFG with decreasing SNR (Bidelman and Howell, 2016). It is possible that the compensatory rightward shifts in response laterality observed by Bidelman & Howell were exaggerated in our sample due to increased age and the presence of hearing loss in some of our listeners (Bidelman et al., 2019b).

Changes in functional connectivity precede measurable behavioral deficits in SIN processing

While no behavioral differences were observed between groups in our SIN detection task (Fig. 1), HL listeners demonstrated enhanced efferent β connectivity when processing SIN (Fig. 5). Overall, these data suggest that

ERD reflects "active information processing" related to excitatory rather than inhibitory processes in the brain and that this desynchronization is likely related to more generalized attentional demands required for the completion of a task. Furthermore, they posited that ERD may play a role in the release of inhibition related to spreading activation. Likewise, Proskovec et al. (2019) found greater decreases in α activation in high- compared to low-load conditions during a verbal working memory task. Attentional models further suggest that increasing task complexity, or cognitive load, leads to improved performance due to greater attentional focus (Kahneman, 1973) and requires higher levels of processing and attentional selection (Lavie, 1995; Lavie et al., 2004). Therefore, it is possible that our SIN detection task was less challenging, requiring less attentional and other neural resources, for listeners who showed greater α coherence during clean speech (those to left side of graph; Fig. 4) compared to listeners who were "low α modulators." However, when greater cognitive resources are required dur-

central compensation through the recruitment of additional, non-canonical auditory brain areas help overcome peripheral deficits to assist older adults' speech perception in noise (e.g., central gain compensation; Chambers et al., 2016). Numerous studies have described age-related changes in both brain structure and function, including inter-regional connectivity (Betzel et al., 2014; Bidelman et al., 2019a; Bidelman et al., 2019b; Grady, 2012; Sullivan and Pfefferbaum, 2006) and compensatory processing (Du et al., 2016; Grady, 2012; Park and McDonough, 2013). Hearing loss is thought to exacerbate the effects observed in typical aging (Lin et al., 2014; Pichora-Fuller and Levitt, 2012; Wayne and Johnsrude, 2015). In fact, studies have shown that increased recruitment of frontal cortical regions is associated with morphological changes particularly in auditory regions, and this additional recruitment has been further linked to behavioral performance (Tyler et al., 2010; Wong et al., 2009). Specifically, our results show enhanced connectivity directed from IFG to PAC in noise suggesting increased neural signaling from linguistic to auditory sensory areas in hearing-impaired listeners. Previous studies have shown IFG contributes to "top-down" processing of speech in more adverse listening conditions (Binder et al., 2004; Zekveld et al., 2006), and it has also been associated with other cognitive functions like working memory (Crinion et al., 2003; Specht et al., 2000) and template matching of the input stimulus to an internal representation within auditory memory (Zekveld et al., 2006). These processes are critical for SIN perception and may account for the hearing-related changes we find in IFG → PAC signaling.

Our data suggest that functional connectivity may perhaps provide a more sensitive measure of changes induced by hearing loss than behavioral measures. The recruitment of frontal sources in aging adults and those with hearing loss may reflect broader alterations within functional networks and compensatory cortical reorganization (Campbell and Sharma, 2013; Cardin, 2016). The stronger efferent (IFG → PAC) connectivity we observed in HL listeners suggests that even mild degrees of hearing loss can alter functional communication between cortical regions subserving speech-language functions. Such changes in functional connectivity may provide a means by which older adults with hearing loss could compensate for impoverished representations in auditory cortices.

Top-down β connectivity increases in strength with poorer hearing

Older adults with hearing loss demonstrated stronger β connectivity in noise between frontal and auditory regions (Fig. 5A), which also scaled with greater degrees of hearing impairment (Fig. 5B). Because no differences were observed in RTs between clean and noise-degraded conditions for either group (Fig. 1C), strengthened β connectivity is unlikely attributed to changes in general listening effort. Rather, we interpret these data to reflect alternative cognitive processing strategies that are utilized with impoverished auditory inputs. This notion aligns with previous studies that have

related oscillatory β-band activity to cognitive processes associated with task demands including working memory (Shahin et al., 2009; Zarahn et al., 2007), encoding and integrating sensory information (Brovelli et al., 2004; von Stein and Sarnthein, 2000; Wang et al., 2017), speech template matching (Bidelman, 2015; Bidelman, 2017; Shahin et al., 2009; Yellamsetty and Bidelman, 2018), as well as predictive coding (Cope et al., 2017; Sedley et al., 2016).

Predictive coding utilizes prior knowledge and experience to form top-down predictions that assist in perception (Friston, 2005; Rao and Ballard, 1999) particularly when sensory inputs are degraded (Cope et al., 2017). Specifically, β-band activity has been related to the updating and precision of predictions (Cope et al., 2017; Sedley et al., 2016) and top-down signaling during speech processing (Fontolan et al., 2014; Wang, 2010). Under a predictive coding framework, fronto-temporal interactions would tend to increase in cases of degraded sensory information (Cope et al., 2017). Aging is associated with increased activation of frontal and motor cortex that helps compensate for impaired SIN perception in older adults (Bilodeau-Mercure et al., 2015; Du et al., 2016). Older listeners also show greater specificity of phoneme representations in frontal articulatory regions compared to auditory brain areas (Du et al., 2016). The increased IFG-PAC connectivity we find could reflect predictive coding that would naturally need to be stronger in listeners who have impoverished sensory encoding (i.e., HL listeners). The fact that this predictive inferencing is restricted to the β-band suggests the "top-down" mechanism observed here is not general attention or listening effort per se (which would be expected in α-band) but template matching and/or interactions between higher (IFG) and lower (PAC) order speech representations.

Additional studies have shown that older adults with hearing loss demonstrate reduced cognitive reserve which impacts higher order language processing as well as other complex processing and tasks that rely heavily on cognitive resources (i.e., SIN) (Cardin, 2016; Mishra et al., 2013; Mishra et al., 2014; Rudner et al., 2009). Furthermore, lower cognitive reserve has been related to higher functional connectivity (Lopez et al., 2014), which in turn is related to perceptual SIN abilities (Bidelman et al., 2019a; Bidelman et al., 2019b; Giordano et al., 2017). Because observed increases in functional connectivity only occurred in noise, it is likely that the increased task demands of more difficult listening conditions further reduced the spare capacity of available cognitive resources in HL listeners leading to the recruitment of frontal regions to overcome depleted sensory resources. The increased efferent connectivity within the β-band may reflect the online recruitment of these additional resources (e.g., IFG) to bolster the matching of sound to speech templates and facilitate SIN comprehension. Alternatively, increased prefrontal activity/connectivity in older, hearing-impaired adults might instead reflect non-specific neural responses (i.e., arousal, attention) rather than compensation via recruitment of specific complementary neural regions to benefit task performance (Morcom and Henson, 2018).

In summary, our findings suggest that α desynchronization in challenging listening conditions reflects a release from inhibition contributing to better SIN performance. This finding supports the notion that a decrease in α functions to assist in active cognitive processing of task-relevant inputs. Additionally, even mild degrees of hearing loss in older adults result in neurophysiological changes in connectivity between cortical auditory and linguistic areas during SIN processing despite negligible behavioral deficits. That this top-down connectivity is restricted to β band suggests hearing loss increases the need to make high-order inferences on noisier sensory representations. Collectively, our findings suggest that functional connectivity is more sensitive to hearing-related changes than region-specific activation and that neural signaling is altered prior to observable behavioral changes. These results emphasize the importance of compensatory, top-down signal transmission in impaired systems to aid SIN perception.

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AUTHOR CONTRIBUTIONS

C.A. collected the data, C.N.P. and G.M.B. analyzed the data; all authors contributed to the interpretation of the results and the writing of the manuscript.

CONFLICT OF INTEREST

The authors declare no competing financial interests.

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