

RESEARCH ARTICLE | *Sensory Processing*

Age-related differences in binaural masking level differences: behavioral and electrophysiological evidence

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Anderson S, Ellis R, Mehta J, Goupell MJ. Age-related differences in binaural masking level differences: behavioral and electrophysiological evidence. *J Neurophysiol* 120: 2939–2952, 2018. First published September 19, 2018; doi:10.1152/jn.00255.2018.—The effects of aging and stimulus configuration on binaural masking level differences (BMLDs) were measured behaviorally and electrophysiologically, using the frequency-following response (FFR) to target brainstem/midbrain encoding. The tests were performed in 15 younger normal-hearing (<30 yr) and 15 older normal-hearing (>60 yr) participants. The stimuli consisted of a 500-Hz target tone embedded in a narrowband (50-Hz bandwidth) or wideband (1,500-Hz bandwidth) noise masker. The interaural phase conditions included NoSo (tone and noise presented interaurally in-phase), NoS π (noise presented interaurally in-phase and tone presented out-of-phase), and N π So (noise presented interaurally out-of-phase and tone presented in-phase) configurations. In the behavioral experiment, aging reduced the magnitude of the BMLD. The magnitude of the BMLD was smaller for the NoSo–N π So threshold difference compared with the NoSo–NoS π threshold difference, and it was also smaller in narrowband compared with wideband conditions, consistent with previous measurements. In the electrophysiology experiment, older participants had reduced FFR magnitudes and smaller differences between configurations. There were significant changes in FFR magnitude between the NoSo to NoS π configurations but not between the NoSo to N π So configurations. The age-related reduction in FFR magnitudes suggests a temporal processing deficit, but no correlation was found between FFR magnitudes and behavioral BMLDs. Therefore, independent mechanisms may be contributing to the behavioral and neural deficits. Specifically, older participants had higher behavioral thresholds than younger participants for the NoS π and N π So configurations but had equivalent thresholds for the NoSo configuration. However, FFR magnitudes were reduced in older participants across all configurations.

NEW & NOTEWORTHY Behavioral and electrophysiological testing reveal an aging effect for stimuli presented in wideband and narrowband noise conditions, such that behavioral binaural masking level differences and subcortical spectral magnitudes are reduced in older compared with younger participants. These deficits in binaural processing may limit the older participant's ability to use spatial cues to understand speech in environments containing competing sound sources.

aging; binaural masking level difference; frequency-following response; perception

INTRODUCTION

Understanding speech in background noise is a major difficulty for older individuals. This difficulty may arise in part from decreased ability to utilize the spatial cues that are thought to provide a large benefit in understanding speech in background noise (Dubno et al. 2008; Peissig and Kollmeier 1997). One method of assessing binaural hearing performance is to compute the improvement in tone detection thresholds when interaural differences are introduced in the stimuli, known as the binaural masking level difference (BMLD). Specifically, a BMLD can be measured when comparing the threshold for an interaurally in-phase tone that is detected in an interaurally in-phase noise (called NoSo) with the threshold for an interaurally out-of-phase tone that is detected in an interaurally in-phase noise (called NoS π) or interaurally in-phase tone that is detected in an interaurally out-of-phase noise (called N π So). A BMLD exists when the NoS π or N π So threshold is lower than the NoSo threshold, demonstrating the benefit of binaural processing. An understanding of age-related changes in the BMLD and in the neural mechanisms that may contribute to these changes may help to explain some of the difficulties that older adults experience when trying to understand speech in noisy environments.

Behavioral Evidence

BMLDs have been studied extensively in humans, and the magnitude of the BMLD is affected by stimulus and subject factors. For example, target tone frequency and bandwidth (BW) are two stimulus factors that affect BMLDs. Increasing the target tone frequency causes increased NoS π and N π So thresholds but does not affect NoSo thresholds, resulting in smaller BMLDs (Goupell 2012; van de Par and Kohlrausch 1999). For a constant overall masking noise level, increasing the BW decreases NoSo thresholds, whereas NoS π thresholds increase with increasing BW, resulting again in smaller BMLDs (Goupell 2012).

Hearing loss and aging are two subject factors that may also reduce the size of the BMLD. Listeners with hearing loss have relatively smaller BMLDs than those with normal hearing (Hall et al. 1984; Jerger et al. 1984; Staffel et al. 1990). Age-related reductions in BMLDs are also well documented in studies comparing younger and older participants with clinically normal hearing (Grose et al. 1994; Pichora-Fuller and Schneider 1992; Pichora-Fuller and Schneider 1998; Pichora-Fuller and Schneider 1991; Strouse et al. 1998), suggesting the

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possibility of a central neural basis for these aging effects. Other studies, however, did not find age-related reductions in BMLDs (Dubno et al. 2008; Kelly-Ballweber and Dobie 1984; Novak and Anderson 1982).

Physiological and Electrophysiological Evidence

Previous studies have investigated the neural mechanisms that could contribute to the BMLD phenomenon in animal and human models. Animal studies have demonstrated that neurons in the inferior colliculus (IC) neurons are tuned to interaural time differences (ITDs) (Kuwada and Yin 1983; Palmer et al. 1990). Changes in the firing rate of these ITD-tuned neurons may contribute to improved behavioral thresholds for NoS π and N π So configurations compared with the NoSo configuration observed in humans. Palmer et al. (2000) measured changes in firing rates in guinea pigs to a 500-Hz tone presented in either NoSo or N π So configurations and found an increase in the single-neuron discharge rate in the N π So condition. However, the firing rate to a target tone does not consistently change in the positive direction for out-of-phase configurations. Jiang et al. (1997a) compared IC neuronal firing rates in NoSo and NoS π configurations and found that the NoS π configuration can increase or decrease neuronal firing rate compared with NoSo, suggesting that at the single-neuron level the change in firing rate rather than the direction of the change may be an important cue for signal detection.

Although single-neuron recordings in the IC have revealed changes in neural firing rates based on interaural configuration, it has been more difficult to measure concomitant changes between interaural configuration and the electrical activity measured from human far-field electrophysiological recordings. When comparing different configurations in polarity, most electrophysiological studies in humans have observed significant changes in evoked potentials arising from cortical but not brainstem structures. For example, Wong and Stapells (2004) measured cortical and brainstem evoked potentials in young normal-hearing (YNH) participants using the auditory steady-state response (ASSR) to a 500-Hz tone presented in 200-Hz BW narrowband (NB) noise. With the use of modulation rates that preferentially drive cortical activity (7 or 13 Hz) or brainstem activity (80 Hz), the 7-Hz rate ASSR amplitude increased for the NoS π configuration relative to the NoSo configuration, but no amplitude differences were found between the NoSo and the NoS π configurations, or between any of the configurations when using the 80-Hz rate. Similarly, using 500-Hz tone bursts presented in wideband (WB) noise, Fowler and Mikami (1996) obtained lower thresholds in the cortical response in the NoS π configuration compared with the NoSo configuration, but they did not find threshold differences between configurations in the middle latency response.

The scalp-recorded frequency-following response (FFR) may be a suitable measure of changes between interaural configurations that reflects binaural processing in brainstem/midbrain. Moushegian et al. (1973) first demonstrated that the FFR could be recorded from the vertex of the human scalp in response to sine tones over a wide range of durations. The FFR reflects sustained sound-evoked activity emanating from multiple generators (Coffey et al. 2016; Coffey et al. 2017; Holmes et al. 2018; Smith et al. 1975; Tichko and Skoe 2017). Responses to frequencies above 100 Hz are likely to emanate

from subcortical generators (Bidelman 2018; Holmes et al. 2018; Tichko and Skoe 2017); therefore, the FFR to a 500-Hz pure tone should reflect brainstem processing. The FFR depends on synchronous phase-locked activity to the periodicity of the stimulus (Marmel et al. 2013); therefore, age-related pathologies that disrupt the precision of neural synchrony will be reflected in reduced FFR amplitudes (Anderson et al. 2012; Clinard et al. 2010; Presacco et al. 2016). Wang and Li (2015) investigated binaural processing in a rat model using the FFR and found that changes in interaural correlation of NB noise stimuli presented to each ear resulted in changes in FFR amplitude. Based on these studies demonstrating FFR sensitivity to effects of aging and changes in binaural stimulation, it is expected that the FFR may be a suitable measure of age-related deficits in binaural processing.

There are two noteworthy studies that found significant FFR differences between interaural configurations. Wilson and Krishnan (2005) used a 500-Hz tone presented in a 1.5-kHz low-pass masker and found significant magnitude increases in both NoS π and N π So configurations relative to the NoSo configuration in the FFR. Clinard et al. (2017) used a 500-Hz tone presented in one-third octave noise centered on 500 Hz to obtain FFR tone-in-noise detection thresholds and found that thresholds were higher in the NoS π configuration compared with the NoSo configuration but thresholds were not significantly different between the N π So and NoSo configurations. FFR amplitude differences between the NoSo and NoS π configurations related to behavioral BMLDs in a subset of the listeners, suggesting a neural correlate of the BMLD in the FFR.

The FFR studies we reviewed did not include aging as a factor in EEG recordings. Using cortical auditory-evoked potentials (CAEPs), however, Eddins and Eddins (2018) obtained behavioral and neural thresholds to 500- and 4,000-Hz tones presented in 50-Hz wide maskers in NoSo and NoS π configurations in 10 YNH, 10 older normal-hearing (ONH), and 10 older hearing-impaired participants. The younger participants had significant larger perceptual BMLDs and larger CAEP threshold differences between configurations than the ONH and older hearing-impaired participants for the 500-Hz tone but not for the 4,000-Hz tone. Furthermore, the CAEP threshold differences between configurations were highly correlated with perceptual BMLDs in all three groups. The authors concluded that the age-related reductions in BMLDs are due to decreased ability to benefit from the temporal fine structure cues that would be available in the 500-Hz tone but not the 4,000-Hz tone (due to phase-locking limits of the auditory system).

We wanted to determine if age-related deficits in BMLDs and temporal processing arise from earlier levels of the auditory system in the brainstem/midbrain. Here, we measured the effects of age, stimulus configuration, and BW on behavioral BMLDs and electrophysiological FFR magnitudes. Temporal processing deficits have been previously demonstrated in human aging subcortical and cortical studies (Mamo et al. 2016; Ozmeral et al. 2016a, 2016b; Presacco et al. 2016). The BMLD depends on precise encoding of interaural timing and level differences; therefore, we predicted that age-related temporal processing deficits would lead to a reduction in FFR magnitude between interaural configurations in older compared with younger participants. Because previous studies have demonstrated effects of BW on the BMLD (Fowler and Mikami 1992;

Goupell 2012; van de Par and Kohlrausch 1999), we also evaluated interacting effects of aging and BW. We used a WB stimulus to facilitate comparisons with previous studies, and we used a NB stimulus to maintain energy within a single filter. This approach may help to explain the age-related reductions in BMLD magnitude found in previous studies.

MATERIALS AND METHODS

Experiment 1: Behavioral

Participants. The participants were 15 YNH (range = 19–26 yr; mean = 22.6 ± 2.2 yr; 4 men) and 15 ONH adults (range = 61–73 yr; mean = 65.1 ± 3.3 yr; 5 men) recruited from the greater Washington, DC metropolitan area. They had clinically normal hearing [audiometric thresholds ≤ 25 -dB hearing level (HL) from 125 to 4,000 Hz bilaterally and air-bone gaps ≤ 10 -dB HL]. In addition, the participants had interaural asymmetries ≤ 15 -dB HL at all tested frequencies and had interaural asymmetries ≤ 5 -dB HL at 500 Hz, the frequency of the target tone in this study. They had type “A” tympanograms following a screening using a Tympanometer System with a 226-Hz probe tone. Participant hearing thresholds are shown in Fig. 1. Note that the thresholds for 500 Hz did not differ between the groups ($P = 0.13$), but significant differences occurred for all frequencies above 500 Hz ($P < 0.01$).

All participants passed cognitive screening using both the Wechsler Abbreviated Scale of Intelligence (WASI; Zhu and Garcia 1999) and the Montreal Cognitive Assessment (Nasreddine et al. 2005) quick screening tests. They had normal IQ scores (≥ 85 on the WASI). The groups did not significantly differ in sex (Fisher’s exact test, $P = 1.00$) or IQ ($P = 0.61$).

All procedures were approved by the University of Maryland’s Institutional Review Board. All participants gave informed, written consent and were compensated for their time.

Stimuli. The target was a 500-Hz tone. It had a 110-ms duration and was temporally windowed by a Hanning window with a 10-ms rise-fall time. The masking noise had a 200-ms duration and was temporally windowed by a Hanning window with a 10-ms rise-fall time. The noise had one of two BWs. The relatively NB noise was a Gaussian white noise with a 50-Hz BW arithmetically centered on 500 Hz. The other noise stimulus was a low-pass Gaussian white noise with frequencies up to 1,500 Hz, a relatively WB noise compared with the 50-Hz BW, which was generated such that there was an infinitely steep slope at 1,500 Hz. For simplicity, we refer to the 50-Hz BW

condition as NB and to the 1,500-Hz low-pass noise as WB. For each BW, a single instance of the noise was used because of the subsequent electrophysiological recordings, during which we wished to reduce sources of variability. When combined, the target tone was temporally centered in the noise. The target tone and noise were tested in three interaural configurations: NoSo, NoS π , and N π So. Figure 2 displays stimulus waveforms and spectra WB noise and NB noise.

Equipment. The participants were presented stimuli that were generated on a personal computer running MATLAB (The Mathworks, Natick, MA). The stimuli were delivered by a Tucker-Davis Technologies System 3 (RP2.1, HB7, PA5; Alachua, FL) and a pair of insert earphones (ER2; Etymotic, Elk Grove Village, IL).

Procedure. Participants viewed a computer monitor with a graphical user interface implemented in MATLAB, which contained three boxes labeled 1, 2, and 3. They initiated a trial with a button press, which was followed by a series of three sounds. The three sound intervals had a 500-ms interstimulus interval (ISI). The participants were instructed to select the interval with the target tone. The first interval was always a reference interval that had no target tone. The target tone was in the second or third interval, randomly chosen on each trial with a priori probability of 50%. The boxes were highlighted during each interval. The participants responded by clicking either the second or third response box. Correct answer feedback was provided after each trial by highlighting the box corresponding to the correct interval.

Thresholds were measured using a three-interval-two-alternative forced-choice staircase procedure using binaural stimulation. The staircase procedure followed a three-down-one-up adaptive rule (Levitt 1971). Four staircases were measured for each condition. The staircases occurred simultaneously, and one of these four staircases was randomly chosen for any given trial until the staircase reached the appropriate number of trials (30 for the quiet condition and 60 for the noise condition). In quiet, the level of the tone was adapted and the level of the target tone started at 40-dB SPL. After the measurement of threshold in quiet, thresholds in noise were measured. In the noise condition, the noise was presented at a fixed level [55-dB sensation level (SL) ranging from 11- to 29-dB SPL in the YNH group and from 16- to 30-dB SPL in the ONH group] and the level of the tone was adapted. The overall level of the tone started at a -10 -dB signal-to-noise ratio (SNR). The adaptive step size was 8 dB for the first two reversals, 4 dB for the next two reversals, 2 dB for the next two reversals, and 1 dB for the rest of the staircase. Four thresholds were obtained for each condition by averaging the reversals of each staircase.

The final threshold was the average of the thresholds for the individual staircases unless there was a >3 -dB standard deviation for the measurements. In that case, one threshold was omitted to minimize the standard deviation (i.e., the final threshold was calculated from the three thresholds that produced the least variability).

There were 30 trials per staircase for measuring tone thresholds in quiet. There were 60 trials per staircase for measuring tone-in-noise thresholds. The three WB noise conditions were tested first because training effects do not seem to occur for WB conditions (Trahiotis et al. 1990). The three configurations (NoSo, NoS π , and N π So) were tested in a random order for each participant. Then, thresholds were measured for the NB conditions, also in a random order. It was thought that there could be possible training and transfer effects of the WB to the NB conditions, which was why the conditions were ordered in this way.

Data and statistical analyses. The thresholds were averaged to obtain a final threshold for each condition. BMLDs were obtained by subtracting the thresholds for the dichotic conditions (NoS π and N π So) from the threshold for the diotic condition (NoSo).

A three-way repeated-measures analysis of variance (RM-ANOVA) was performed on behavioral thresholds with one between-subjects factor (age, 2 levels: younger and older) and two within-subjects factors (configuration, three levels: NoSo, NoS π , and N π So;

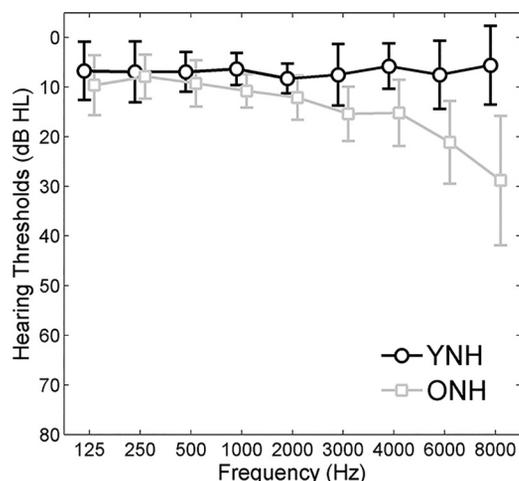


Fig. 1. Average hearing thresholds for right and left ears are plotted from 125 to 8,000 Hz for young normal-hearing (YNH; black circles) and older normal-hearing (ONH; gray squares) participants. HL, hearing level. Error bars = ± 1 SD.

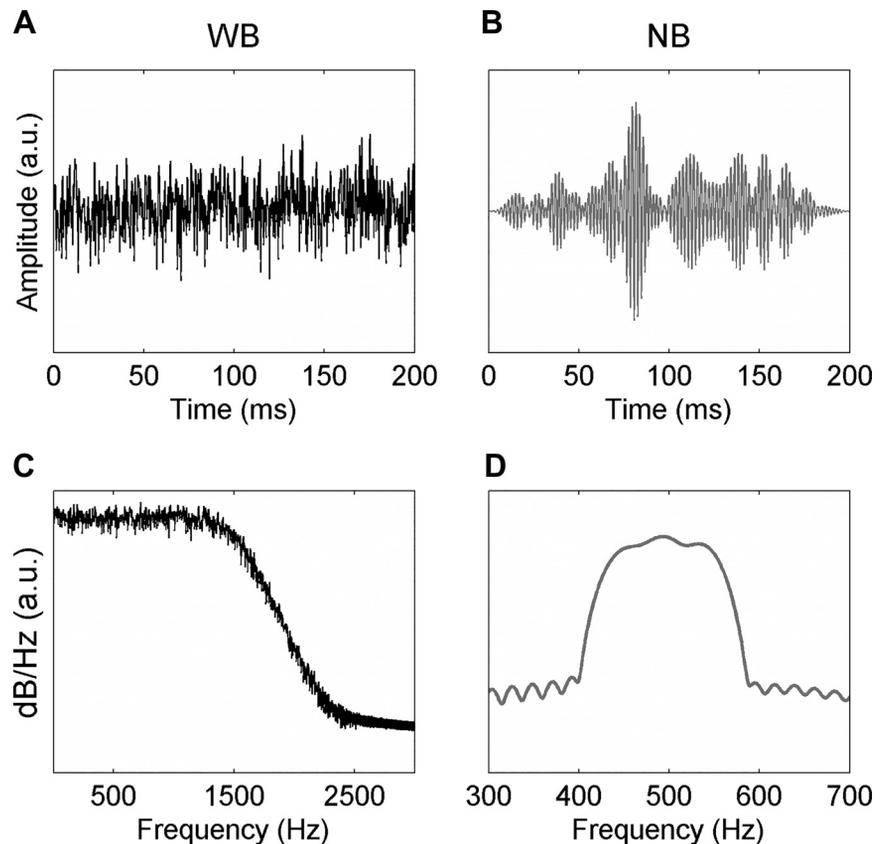


Fig. 2. Stimulus waveforms and spectra are displayed for of a single frozen iteration of each of the wideband (WB; A and C) and narrowband (NB; B and D) noise stimuli. These particular stimuli were used for all experiments; a.u., arbitrary units.

BW, two levels: WB and NB) to determine the effects of age and BW on the thresholds. A separate three-way RM-ANOVA was performed on the BMLDs with factors age, BW, and configuration; this time there were two configuration levels (BMLD = NoSo–NoS π , and BMLD = NoSo–N π So). The false discovery rate procedure (Benjamini and Hochberg 1995) was applied to control for multiple comparisons for main effects.

Experiment 2: FFR

Participants. The participants were the same as those tested in experiment 1.

Stimuli and recording. The stimuli used to obtain the behavioral BMLDs were also used in the FFR experiment, a 110-ms 500-Hz tone and masking noise that had either a BW of 50-Hz centered on 500 Hz (NB) and a relatively WB noise with energy up to 1,500 Hz (WB). Note that a single instance of each noise stimulus was used during the recordings. To perform the FFR experiment, a binaural behavioral threshold was first obtained for the 500-Hz tone burst by presenting the tone using Presentation software (Neurobehavioral Systems, Berkeley, CA) through ER-1 insert earphones (Cortech, Wilmington, NC) using the Hughson-Westlake procedure. For the NoSo condition, identical tone and noise stimuli were presented in each ear. For the NoS π and N π So conditions, the polarity of the tone or noise waveforms was presented in inverting polarities between the ears, respectively.

During the recording, the 500-Hz tone was presented binaurally at 55-dB SL through ER-1 insert earphones at a rate of 4.76 Hz and the WB and NB stimuli were presented at -10 -dB SNR in a continuous loop. An additional set of recordings was recorded in 10 young participants in which the NB stimuli were presented with the same 100-ms ISI as the 500-Hz tone. FFRs were recorded using the Biosemi ActiveTwo acquisition system (Cortech Solutions, Wilmington, NC) at a sampling rate of 16,384 Hz. Recordings were made for the tone

in quiet (So) and the tone in WB and NB noise in each interaural configuration (NoSo, NoS π , and N π So), for a total of seven conditions. To determine the effects of phase configuration on representation of the tone, in 12 additional participants (7 from the younger and 5 from the older groups), FFRs were recorded to the tone in quiet in the dichotic condition (S π). FFRs were recorded differentially with a two-channel, vertical montage with Cz serving as the active electrode and linked earlobes as references. In addition, a common mode sense active electrode and a driven right leg passive electrode were placed on the forehead to reduce common-mode interference. All electrode offsets were <40 mV. A criterion of ± 50 μ V was used for online artifact rejection, and a single run of 2,200 artifact-free sweeps was collected for each condition. During the recording, participants sat in a comfortable chair and watched a muted captioned movie of their choice to facilitate a quiet but alert mental state. A control recording was done with blocked tubing to ensure that the FFR was not contaminated by stimulus artifact. While better SNRs may be obtained while participants are sleeping, we find that some participants, especially the older ones, are not able to maintain a stable sleep state for up to 2 h, and excessive noise may result when participants vary between sleeping and wake states.

Data reduction and analyses. Responses were digitally filtered offline from 460 to 540 Hz using a second-order Butterworth filter and responses were epoched from -47 to 110 ms, referenced to the stimulus onset. Any sweep with amplitude >30 μ V was rejected as artifact and the final average comprised the first 2,000 artifact-free sweeps. SNR in dB was calculated using the following formula:

$$\text{SNR} = 20\log_{10}(\text{RMS poststimulus} / \text{RMS prestimulus})$$

where the poststimulus period is defined as 0–110 ms and the prestimulus period (i.e., noise) is defined as -47 –0 ms and RMS is root mean square. Any individual that had an SNR <0.5 dB in the So condition was asked to return for testing. Two YNH participants and one ONH participant were retested and had SNRs that met criteria

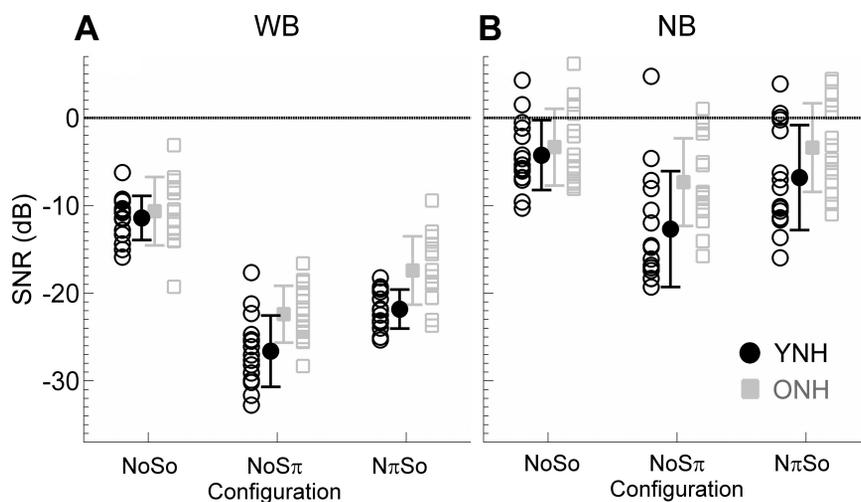


Fig. 3. Thresholds for the wideband (WB; A) and narrowband (NB; B) noise conditions for younger (circles) and older (squares) participants. Open symbols show the individual thresholds; closed symbols show the average thresholds with error bars that are ± 1 SD in length. NoSo, tone and noise presented interaurally in-phase; NoS π , noise presented interaurally in-phase and tone presented out-of-phase; N π So, noise presented interaurally out-of-phase and tone presented in-phase.

during the second test session. Spectral magnitudes were calculated from each response using fast Fourier transforms with one 20-Hz bin centered around 500 Hz over the time response region (5–100 ms).

Statistical analyses. A three-way RM-ANOVA was performed on FFR magnitude of the response to 500 Hz with one between-subjects factor (group, 2 levels: younger and older) and two within-subjects factors (configuration, 3 levels: NoSo, NoS π , and N π So; BW, 2 levels: WB and NB). The false discovery rate procedure (Benjamini and Hochberg 1995) was applied to control for multiple comparisons for main effects.

RESULTS

Experiment 1

Thresholds for the 500-Hz tone in quiet were significantly lower by 4 dB on average for the YNH participants (17.7 ± 5.6 dB SPL) compared with the ONH participants (21.7 ± 4.4 dB SPL) (two-tailed two-sample *t*-test assuming equal variances; $P = 0.035$).

Figure 3 shows the individual and average tone-in-noise thresholds for the three interaural configurations. Thresholds were significantly higher for the ONH participants compared with the YNH participants [main effect age: $F(1,28) = 5.57$, $P = 0.025$, $\eta_p^2 = 0.17$]. There was a significant main effect of configuration on thresholds [$F(2,28) = 203$, $P < 0.0001$, $\eta_p^2 = 0.17$], such that NoSo thresholds were higher than NoS π and N π So thresholds and N π So thresholds were higher than NoS π thresholds for both WB and NB noise. Thresholds were significantly higher for the NB noise compared with the WB noise [main effect BW: $F(1,28) = 458$, $P < 0.0001$, $\eta_p^2 = 0.94$]. There was a significant age \times configuration interaction [$F(2,78) = 8.31$, $P = 0.002$, $\eta_p^2 = 0.38$], arising from larger differences between configurations in YNH than in ONH.

Figure 4 shows the average BMLDs, derived from the difference between the diotic and dichotic thresholds. BMLDs were significantly smaller for the ONH participants compared with the YNH participants [main effect age: $F(1,28) = 368$, $P < 0.0001$, $\eta_p^2 = 0.93$] and were significantly larger when derived from the NoSo–NoS π thresholds than when compared with the BMLDs derived from the NoSo–N π So thresholds [$F(2,28) = 86.4$, $P < 0.0001$, $\eta_p^2 = 0.76$]. Finally, BMLDs were significantly larger for the WB noise compared with the NB noise [main effect BW: $F(1,28) = 132$, $P < 0.0001$,

$\eta_p^2 = 0.83$]. Table 1 displays average group thresholds and BMLDs.

Figure 3 shows significant interactions for the thresholds (age \times configuration and BW \times configuration, $P < 0.0005$ for both), but Fig. 4 shows no significant interactions for the BMLDs ($P > 0.05$ for all). There were no age-related differences in NoSo thresholds; the age-related threshold increases were for the NoS π and N π So configurations only, resulting in smaller BMLDs across conditions and demonstrating an age-related binaural processing deficit that was approximately equal across configurations and BW conditions. Thus all BMLD interactions were not significant.

Experiment 2

Effects of aging. Figure 5 displays FFR response amplitudes and spectra for YNH and ONH participants for the NoSo, NoS π , and N π So conditions in WB and NB conditions when the tone is presented in a continuous noise background. FFR magnitudes are also compared for So and S π (7 YNH and 5 ONH participants). FFR magnitudes were lower in ONH compared with YNH participants [$F(1,28) = 3.8$, $P = 0.038$, $\eta_p^2 = 0.15$]. There was a significant age \times configuration \times BW interaction [$F(2,27) = 6.7$, $P = 0.004$, $\eta_p^2 = 0.33$].

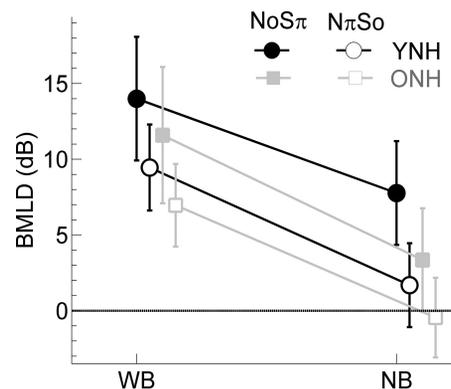


Fig. 4. Group average perceptual binaural masking level differences (BMLDs) for young normal-hearing (YNH; black circles) and older normal-hearing (ONH; gray squares) groups for noise presented interaurally in-phase and tone presented out-of-phase (NoS π ; closed symbols) and noise presented interaurally out-of-phase and tone presented in-phase (N π So; open symbols) configurations. Error bars are ± 1 SD in length. WB, wideband; NB, narrowband.

Table 1. Average group thresholds for the 500-Hz tone in quiet and in three phase configurations (NoSo, NoS π , and N π So) in WB and NB noise

Group/Bandwidth	Threshold, dB SPL				BMLD, dB	
	Quiet	NoSo	NoS π	N π So	NoSo-NoS π	NoSo-N π So
YNH						
WB	17.67 (5.6)	43.57 (2.5)	28.38 (4.1)	33.18 (2.2)	15.20 (3.8)	10.39 (2.8)
NB		50.74 (4.0)	42.31 (6.6)	48.18 (6.0)	8.44 (3.7)	2.56 (2.8)
ONH						
WB	21.73 (4.38)	44.39 (4.1)	32.59 (3.3)	37.58 (3.9)	11.75 (3.3)	6.77 (2.9)
NB		51.65 (4.4)	47.65 (5.0)	51.60 (5.1)	3.90 (2.9)	-0.14 (3.1)

Binaural-masking-level-difference (BMLD) averages (SD) for threshold differences for NoSo–NoS π and for NoSo–N π So for WB and NB noise. YNH, young normal-hearing; ONH, older normal-hearing; WB, wideband; NB, narrowband; NoSo, tone and noise presented interaurally in-phase; NoS π , noise presented interaurally in-phase and tone presented out-of-phase; N π So, noise presented interaurally out-of-phase and tone presented in-phase.

To better understand this interaction, separate two-way RM-ANOVAs were conducted for each BW. There was a significant age \times configuration interaction for each BW [WB: $F(2,27) = 3.4$, $P = 0.048$, $\eta_p^2 = 0.20$; NB: $F(2,27) = 18.63$, $P < 0.001$, $\eta_p^2 = 0.58$]. These interactions were driven by differences between the dichotic and diotic configurations; the differences were larger for the YNH compared with the ONH participants. Specifically, for the WB condition, there was a main effect of configuration in the younger but not the older group [young: $F(2,13) = 12.3$, $P = 0.001$, $\eta_p^2 = 0.65$; older: $F(2,13) = 0.4$, $P = 0.706$, $\eta_p^2 = 0.05$], due to the fact that the changes from the NoSo to NoS π only produced significant changes in FFR magnitudes in the young participants. For the NB configuration, there was a main effect of configuration in both age groups, but the effect size was smaller in the older participants [YNH: $F(2,13) = 15.6$, $P < 0.001$, $\eta_p^2 = 0.71$; ONH: $F(2,13) = 5.4$, $P = 0.020$, $\eta_p^2 = 0.45$]. Figure 6 shows individual and group average values corresponding to the tone-in-noise magnitudes in Fig. 5. In Fig. 7, FFR magnitude differences are displayed as an electrophysiological analog to the perceptual BMLD.

Effects of BW and configuration. Figure 8 shows the effects of noise and phase configuration on the FFR magnitude of 500 Hz in the WB and NB conditions in YNH and ONH participants. The FFR magnitudes were always higher for the So condition than for any other of the other three configurations using WB noise [$F(1,28) = 17.5$, $P < 0.001$, $\eta_p^2 = 0.39$]. In contrast, the FFR magnitudes were higher in the NoS π configuration compared with the So, NoSo, and N π So configurations using NB noise (Table 2). Note that the peak FFR magnitude was observed as expected at 500 Hz for all WB configurations and for the NB N π So configuration. The peak for the NB NoSo and NoS π configurations, however, shifted from 500 Hz to a lower frequency (~491 Hz) in both the YNH and ONH groups, which is expected given the NB spectrum in Fig. 2 that shows that the peak is shifted to a slightly lower frequency (495 Hz). Additional energy is noted in the side lobes surrounding 500 Hz in all NB conditions, consistent with the NB spectrum in Fig. 2 showing additional peaks of energy above and below 500 Hz. For consistency, spectral magnitudes were calculated over a 20-Hz bin surrounding 500 Hz for all conditions, even though the peak

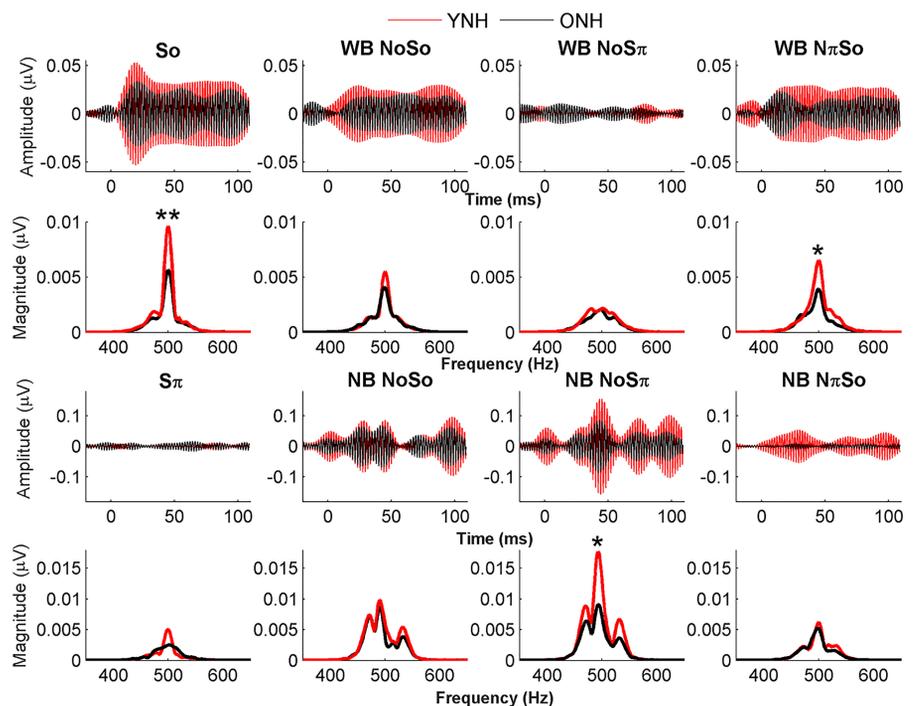


Fig. 5. Effects of aging on frequency-following-response magnitudes and response amplitudes in the various test configurations with continuous background noise. Note that group averages are based on 15 participants for each age group, except for the tone in quiet in the dichotic condition (S π) for which there are 7 participants in the young normal-hearing (YNH) group and 5 participants in the older normal-hearing (ONH) group. NoSo, tone and noise presented interaurally in-phase; NoS π , noise presented interaurally in-phase and tone presented out-of-phase; N π So, noise presented interaurally out-of-phase and tone presented in-phase; So, tone in quiet; WB, wideband; NB, narrowband. * $P < 0.05$, ** $P < 0.01$.

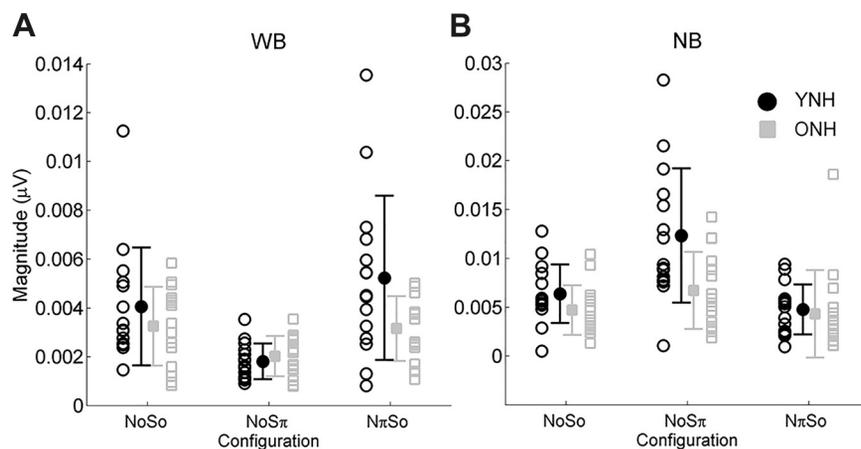


Fig. 6. Frequency-following-response magnitudes for the wideband (WB; A) and narrowband (NB; B) noise conditions for younger (circles) and older (squares) participants. Open symbols show the individual magnitude values; closed symbols show the average magnitude values with error bars that are ± 1 SD in length. NoSo, tone and noise presented interaurally in-phase; NoS π , noise presented interaurally in-phase and tone presented out-of-phase; N π So, noise presented interaurally out-of-phase and tone presented in-phase.

occurred at a lower frequency for NB NoSo and NoS π configurations.

When the differences between the noise configurations were compared, the magnitudes were higher in the NB than in the WB conditions [$F(1,28) = 30.1$, $P < 0.001$, $\eta_p^2 = 0.52$]. There was also a main effect of configuration [$F(2,27) = 5.7$, $P = 0.009$, $\eta_p^2 = 0.30$] and a significant configuration \times BW interaction [$F(2,27) = 28.8$, $P < 0.001$, $\eta_p^2 = 0.67$]. This interaction was driven by changes in magnitude with configuration that reversed direction between the WB and NB conditions. As can be seen in Fig. 9, A and B, WB spectral magnitudes were smaller for the NoS π configuration than for the NoSo configuration [paired t -test: $t(29) = 4.5$, $P < 0.001$, $\eta_p^2 = 0.43$]; in Fig. 9, C and D, the opposite pattern was seen and NB magnitudes were larger for the NoS π configuration than for the NoSo configuration [paired t -test: $t(29) = 5.3$, $P < 0.001$, $\eta_p^2 = 0.37$]. The change from NoSo to N π So was not significant for either WB or NB [paired t -tests: WB: $t(29) = 1.3$, $P = 0.19$; $\eta_p^2 = 0.06$; NB: $t(29) = 1.9$, $P = 0.06$; $\eta_p^2 = 0.12$].

It is interesting that the response magnitude in the NoS π configuration compared with the NoSo configuration was reduced for WB noise (1,500-Hz BW) but was increased for NB noise (50-Hz BW). To further explore the reasons for these differences, the RMS amplitudes were calculated in the pre-stimulus range (-46 to 0 ms) for the NB NoSo and NoS π , and

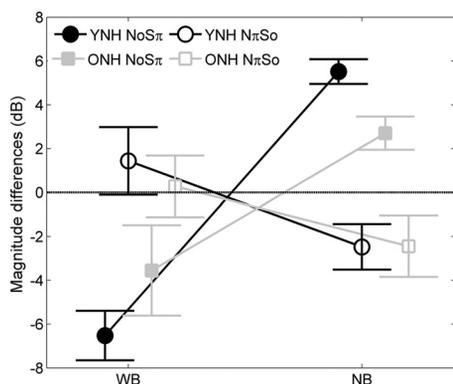


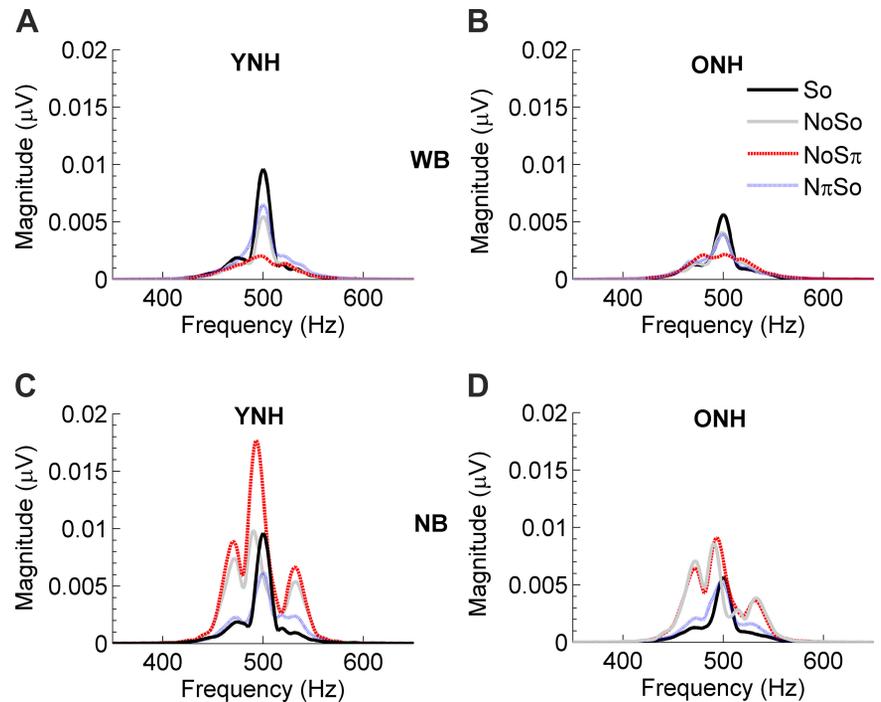
Fig. 7. Frequency-following-response magnitude differences (in dB) between configurations displayed for young normal-hearing (YNH; black circles) and older normal-hearing (ONH; gray squares) participants for noise presented interaurally in-phase and tone presented out-of-phase (NoS π ; closed symbols) and noise presented interaurally out-of-phase and tone presented in-phase (N π So; open symbols) configurations. WB, wideband; NB, narrowband. Error bars are ± 1 SD in length.

WB NoSo and NoS π configurations. Amplitudes in the pre-stimulus range were higher for NB noise than for WB noise [NoSo: $t(29) = 3.1$, $P = 0.004$; NoS π : $t(29) = 3.6$, $P = 0.001$]. We also calculated SNR in the spectral domain by dividing the magnitude corresponding to 500 Hz by the magnitude corresponding to 600 Hz (20-Hz bins for each frequency) in the poststimulus period (5–100 ms). Spectral SNRs were higher for NB noise than for WB noise in the NoS π configuration [$t(29) = 5.4$, $P < 0.001$]. They were also somewhat higher in the NoSo configuration but the difference failed to meet statistical significance [$t(29) = 1.8$, $P = 0.07$]. A RM-ANOVA with spectral SNR as the dependent variable revealed similar results to those obtained with absolute magnitudes. There was a significant configuration \times BW interaction [$F(2,27) = 20.8$, $P < 0.001$, $\eta_p^2 = 0.61$], driven by a change in magnitude from NoSo to NoS π configurations that reversed direction between the WB and NB conditions. This effect may have resulted from the masker spectral content being time locked to the average response.

To reduce possible effects of continuous noise background on FFR magnitudes in the NB condition, an additional 10 YNH participants were tested with the 500-Hz tone and the NB noise of identical durations at the same 4.76-Hz rate. In these participants, responses were recorded to the following stimulus configurations using the NB noise stimuli: So, S π , No, N π , NoSo, NoS π , and N π So. Figure 9 shows that in this condition, magnitudes are reduced for both dichotic phase configurations (NoS π and N π So) compared with the diotic phase configuration (NoSo) [NoS π –NoSo: $t(9) = 2.6$, $P = 0.029$; N π So–NoSo: $t(9) = 2.8$, $P = 0.022$]. The magnitudes are also reduced for S π and N π compared with So and No, respectively [S π –So: $t(9) = 3.0$, $P = 0.014$; N π –No: $t(9) = 2.5$, $P = 0.032$]. Mean FFR magnitudes and standard deviations are shown in Table 3. In summary, compared with the NoSo configuration, magnitudes are increased for NoS π but decreased for N π So in the continuous noise condition (Fig. 8), but magnitudes are decreased for both NoS π and N π So compared with the NoSo configuration in the intermittent noise condition (Fig. 9).

Relationships among behavioral and electrophysiological results. Pearson product-moment correlation coefficients were computed to assess relationships among the behavioral BMLDs and both absolute FFR magnitudes and FFR magnitude differences (subtracted NoS π from NoSo and N π So from NoSo for WB and NB), both for pooled YNH and ONH

Fig. 8. Effects of configuration on frequency-following-response magnitudes in young normal-hearing (YNH; *A* and *C*) vs. older normal-hearing (ONH; *B* and *D*) participants. Grand averaged spectra from individual waveforms are overlaid for tone in quiet (So; black), tone and noise presented interaurally in-phase (NoSo; gray), noise presented interaurally in-phase and tone presented out-of-phase (NoS π ; red dashed), and noise presented interaurally out-of-phase and tone presented in-phase (N π So; blue dotted) in the wideband (WB) and narrowband (NB) conditions.



participants and for subgroups of YNH and ONH participants. No significant correlations were observed ($P > 0.05$ for all). Figure 10 displays scatterplots among perceptual thresholds/FFR magnitudes, and Fig. 11 displays scatterplots among behavioral BMLDs and FFR magnitude differences.

DISCUSSION

Experiment 1

Experiment 1 measured behavioral thresholds for tones in noise. The results shown in Figs. 3 and 4 demonstrate an overall effect of aging (smaller BMLDs in older than in younger participants across conditions), an effect of configuration (smaller BMLDs for the NoSo–N π So difference than for the NoSo–NoS π difference), and an effect of BW (smaller BMLDs for narrow BWs than for wide BWs).

The most important feature of the data in Fig. 3 is that they show that average thresholds are higher for the older participants than for the younger participants but only for the interaurally out-of-phase configurations. This resulted in BMLDs

that were 3.5 dB smaller for the ONH participants compared with the YNH participants (Fig. 4). Therefore, many the older participants do not experience a release of masking associated with interaural phase differences (IPDs) to the same extent as younger participants. These results are consistent with the study of Grose and Mamo (2010) who found that older participants had poorer detection of IPDs than younger participants, even at the relatively low frequencies of 250 and 500 Hz. Recognizing the need to evaluate the independent contributions of age and hearing loss on IPD discrimination, King et al. (2014) evaluated a group of participants who had a wide range of hearing thresholds and ages. They found that age correlated with temporal-fine-structure (TFS) IPD thresholds and envelope IPD thresholds when controlling for hearing thresholds, and hearing thresholds correlated with TFS IPD thresholds, but not envelope IPD thresholds, when controlling for age.

Our results suggest that aging does not affect the ability to detect signals in noise, given equivalent thresholds in the NoSo conditions across BWs. However, older participants show reduced ability to use ITDs/IPDs to improve hearing in noise,

Table 2. Average group 500-Hz magnitudes in quiet (So and S π) and in three phase configurations (NoSo, NoS π , and N π So) in WB and NB noise

Group/Bandwidth	500-Hz Magnitude (μV) $\times 10^3$					Magnitude Differences (μV) $\times 10^3$	
	So	S π	NoSo	NoS π	N π So	NoSo–NoS π	NoSo–N π So
YNH							
WB	7.34 (3.2)	3.22 (1.8)	4.10 (2.4)	1.81 (0.7)	5.24 (3.4)	–2.25 (2.1)	1.17 (2.6)
NB			6.40 (3.0)	12.34 (6.9)	4.77 (2.6)	5.95 (4.6)	–1.62 (2.3)
ONH							
WB	4.29 (2.7)	2.4 (1.9)	3.26 (1.6)	2.02 (0.8)	3.16 (1.3)	–1.23 (2.1)	–0.09 (1.5)
NB			4.71 (2.7)	6.72 (4.0)	4.33 (4.5)	2.01 (2.3)	–0.39 (3.3)

Average group magnitude differences (SD) between NoSo and NoS π and between NoSo and N π So in WB and NB noise. YNH, young normal-hearing; ONH, older normal-hearing; WB, wideband; NB, narrowband; NoSo (tone and noise presented interaurally in-phase), NoS π (noise presented interaurally in-phase and tone presented out-of-phase), and N π So (noise presented interaurally out-of-phase and tone presented in-phase); So, tone in quiet; S π , tone in quiet presented interaurally out-of-phase.

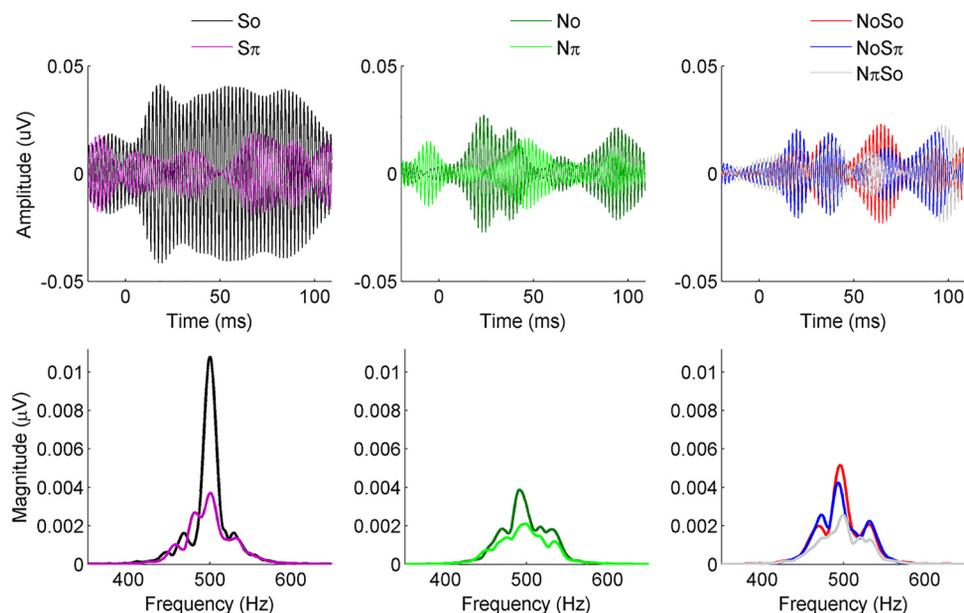


Fig. 9. Grand average response waveforms and spectra derived from individual waveforms are displayed for 10 young normal-hearing (YNH) participants in responses to binaural stimuli presented in phase or 180° out of phase between ears for tone only, narrowband noise only, and tone-in-noise condition. NoSo, tone and noise presented interaurally in-phase; NoS π , noise presented interaurally in-phase and tone presented out-of-phase; N π So, noise presented interaurally out-of-phase and tone presented in-phase; So, tone in quiet; S π , tone in quiet presented interaurally out-of-phase.

consistent with a reduction of temporal processing with age (Pichora-Fuller and Schneider 1991) that is independent of the stimulus presented. We note that some of the older participants outperformed many of the younger participants across conditions. Some of our older listeners had participated in previous perceptual experiments, so they may have acquired listening expertise that enhanced their performance. Furthermore, variable performance is commonly found in binaural experiments (Goupell 2012; Goupell and Barrett 2015), so it is not surprising that some of the older participants would have better performance than the younger participants. Overall, our study provides further evidence that deficient temporal processing, independent of absolute hearing thresholds, contributes to the older participant's hearing difficulties in background noise.

The results mostly confirm previous measurements comparing BMLDs obtained with different BWs. van de Par and Kohlrausch (1999) measured NoSo, NoS π , and N π So thresholds for 500-Hz tones in 50-Hz and 1,000-Hz BW background noises in three highly experienced participants (our WB noise stimuli have a slightly larger but comparable BW). Goupell (2012) measured NoSo and NoS π thresholds for 500-Hz tones in 50-Hz background noise in five trained YNH participants. NoS π and N π So thresholds were better in van de Par and Kohlrausch (1999) and Goupell (2012) than in the current

Table 3. Average group FFR magnitudes for a 500-Hz tone in quiet (So and S π), for a NB noise alone (No and N π), and for three configurations of tone in NB noise (NoSo, NoS π , and N π So) in NB noise for the interrupted noise condition

Magnitude, nV						
So	S π	No	N π	NoSo	NoS π	N π So
8.23	3.09	3.14	1.92	4.15	3.08	2.07
(5.7)	(1.4)	(1.3)	(0.9)	(2.5)	(1.6)	(0.7)

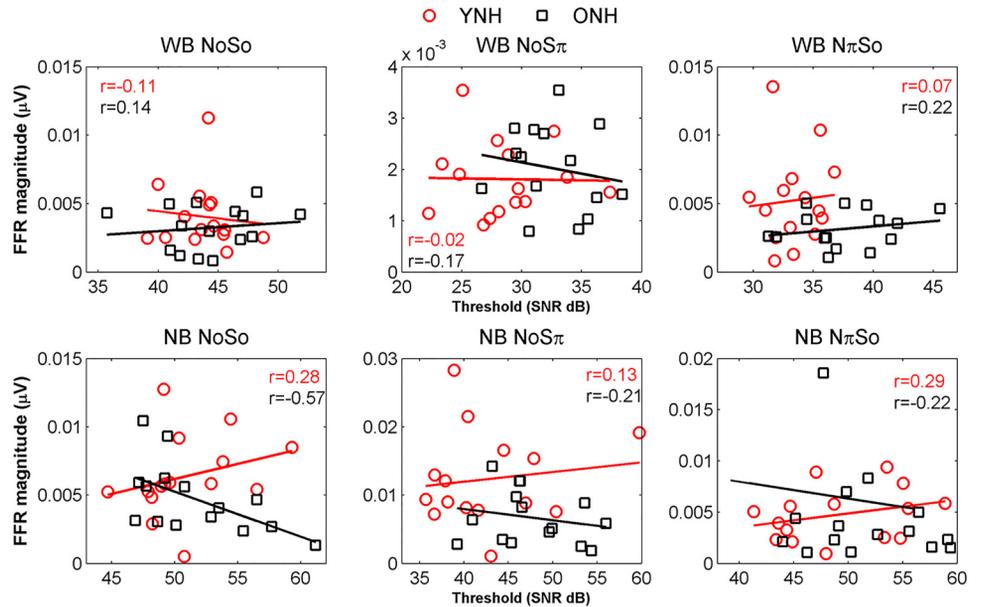
Magnitude differences (SD) are shown. NB, narrowband; So, tone in quiet; S π , tone in quiet in the dichotic condition; No, in-phase noise alone; N π , out-of-phase noise alone; NoSo, tone and noise presented interaurally in-phase; NoS π , noise presented interaurally in-phase and tone presented out-of-phase; N π So, noise presented interaurally out-of-phase and tone presented in-phase.

study, which has several possible explanations. First, those studies targeted threshold at 70.7% correct on the psychometric function, whereas we targeted 79.1% correct, which should produce higher thresholds. Second, our participants may not have been as highly trained as those in the previous studies. We did not include explicit training in our study. Training does not appear to be necessary for the WB conditions (Trahiotis et al. 1990) but may be important for NB conditions, where the largest discrepancies were seen. Third, the number of participants in the current study is much larger than the other studies. It could be that our group of participants showed better generalizability to the larger population. Historically, binaural perception studies included a small number of participants, with the possibility of a bias to recruit experts. We did not recruit experts for the current study because we wanted a wide range of performance with the hopes of being able to correlate behavioral and electrophysiology measurements. The ability to detect interaural decorrelation, the cue used to achieve BMLDs, is quite variable when using narrowband stimuli. For example, Goupell and Barrett (2015) showed that performance in naïve participants can range from being expert like to being unable to detect interaural decorrelation when presented 10-Hz BW, 500-Hz characteristic frequency NB noises. Likewise, some of the participants of this study had much lower thresholds than others. For example, thresholds were as low as -19 - and -16 -dB SNR for the NoS π and N π So conditions, respectively, which is much closer to those previously reported.

Experiment 2

We measured aging effects on FFR magnitudes in diotic and dichotic phase configurations and in BWs (WB vs. NB). Overall, the older participants had smaller FFR magnitudes across conditions (Figs. 5 and 6) and the effects of configuration were reduced in older compared with younger participants (Fig. 7). We also found that the effects of continuous noise on the FFR magnitude to 500 Hz differed for NB vs. WB conditions (Fig. 8). Relative to the quiet condition in WB noise, the 500-Hz FFR magnitude decreased for all phase configurations. In NB noise, however, the FFR magnitude increased for the

Fig. 10. Scatter plots among perceptual thresholds and frequency-following-response (FFR) magnitudes among the younger normal-hearing (YNH; black circles) and older normal-hearing (ONH; gray squares) participants. Note that no correlations were significant after correcting for multiple comparisons. NoSo, tone and noise presented interaurally in-phase; NoS π , noise presented interaurally in-phase and tone presented out-of-phase; N π So, noise presented interaurally out-of-phase and tone presented in-phase; WB, wideband; NB, narrowband.

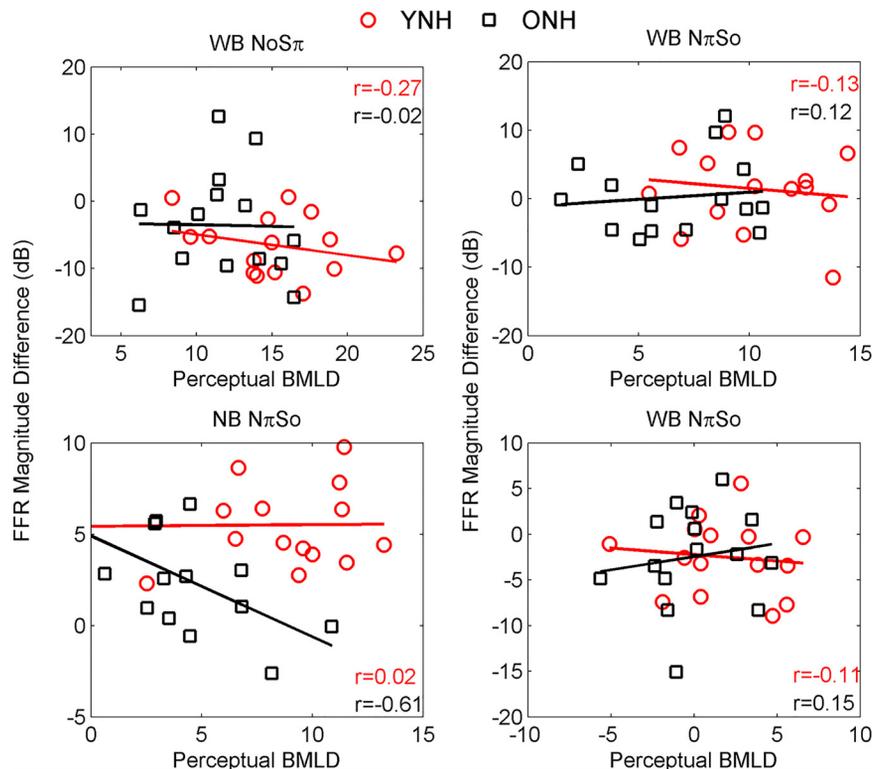


NoSo and NoS π configurations. In the WB condition, FFR magnitudes were decreased in the NoS π compared with the NoSo configuration in both YNH and ONH participants. There was a slight increase in N π So compared with NoSo configurations, but the difference was not significant, possibly due to the large variance of data, especially in the YNH group. The opposite effect occurred in the NB condition; FFR magnitudes were increased in NoS π compared with NoSo configurations but were decreased for the N π So compared with NoSo configurations. We performed an additional experiment to help us to understand these discrepant results and recorded responses to 500 Hz in interrupted noise. These results showed that FFR magnitudes were decreased for all noise and tone-in-noise

conditions relative to the quiet condition, similar to what was seen with WB noise (Fig. 9). Furthermore, FFR magnitude was lower in dichotic vs. diotic configurations for all tone, noise, and tone-in-noise stimulus conditions. Overall, the direction of the effects was similar between age groups. While other studies have investigated neural correlates of the BMLD in electrophysiological studies in young participants, this study is novel in that it also looked at effects of aging and varying BW.

As noted in Fig. 6, the effects of noise were greater in the YNH than in the ONH participants. A steeper decline in FFR magnitude was noted in YNH compared with ONH participants when comparing responses to the tone in quiet to re-

Fig. 11. Scatter plots among behavioral and binaural masking level differences (BMLDs) and frequency-following-response magnitude differences among the younger normal-hearing (YNH; black circles) and older normal-hearing (ONH; gray squares) participants. NoSo, tone and noise presented interaurally in-phase; NoS π , noise presented interaurally in-phase and tone presented out-of-phase; N π So, noise presented interaurally out-of-phase and tone presented in-phase; WB, wideband; NB, narrowband.



sponses to the tone in noise for WB [$F(1,26) = 3.6$, $P = 0.027$, $\eta_p^2 = 0.29$] and NB [$F(1,26) = 4.7$, $P = 0.010$, $\eta_p^2 = 0.35$] conditions. We interpret these findings as an indication of reduced overall neural synchrony that affects the ONH FFRs even in quiet. Because the older participants' responses to the tone in quiet are already degraded, the desynchronizing effects of noise on the FFR are not as great in older participants as in younger participants. These results are similar to those of Presacco et al. (2016), who found reduced effects of noise on FFRs to speech in noise (single talker) in older participants compared with younger participants. Therefore, reduced overall synchrony may be the mechanism underlying the smaller magnitude differences between interaural phase configurations in ONH compared with YNH participants. We note a large variability in FFR magnitudes across both groups of participants. Furthermore, the effects of age were not uniform, and some of the older participants had magnitudes that were equal to or better than many of the younger participants.

The pattern of configuration changes in the YNH participants was similar to that of Clinard et al. (2017) ($n = 14$, mean age 22.6 yr), who measured FFR tone-in-noise physiological thresholds and found that the threshold increased in the WB NoS π configuration compared with the WB NoSo configuration. Both the current study and that of Clinard et al. (2017) showed a decrease in WB NoS π magnitude relative to WB NoSo magnitude but no significant differences between the WB N π So and WB NoSo configurations (Figs. 6–8).

The reduction in magnitude in the NoS π configuration compared with the NoSo configuration has also been found in responses arising from cortex. Ishida and Stapells (2009) recorded the ASSR in young participants ($n = 10$, mean age 27.4 yr) using a 500-Hz tone with a 40-Hz sinusoidal amplitude modulation that was presented in a 200-Hz NB noise in NoSo, NoS π , and N π So configurations. Using this paradigm, Ishida and Stapells (2009) found spectral magnitude differences between the NoSo and NoS π configurations and between the NoSo and the N π So configurations. The authors suggested that the reduction in energy in the dichotic configurations may be in agreement with single-unit studies showing a decrease in firing rate for dichotic stimuli (McAlpine et al. 1996), and they further noted that perhaps this change in firing rate is used by the cortex to improve detection of the target signal.

Not all studies have found a decrease in magnitude in the NoS π compared with the NoSo configuration. Wilson and Krishnan (2005) recorded the FFR in young participants (18–28 yr) to a 500-Hz tone presented at 56-dB SPL in a 1,500-Hz low-pass noise masker that was presented at level that was sufficient to achieve masking of the tone during behavioral testing. They found that response magnitudes increased for both NoS π and N π So compared with the NoSo configuration, with the greatest effects seen for the N π So configuration. The study of Wilson and Krishnan (2005) study employed a strict criterion for inclusion, such that only participants who had a 50% reduction in response amplitude in the NoSo configuration compared with the So amplitude were included. Only 9 of the original 15 participants met this criterion. Because we were interested in examining a broad range of temporal processing abilities across age groups, we chose not to use this criterion. Instead, our criterion for inclusion was simply that the magnitude of the response to the tone

exceeded the magnitude of the noise floor (the prestimulus region).

We did not find any correlations among the behavioral and physiological findings. We note that the procedures were not identical between the behavioral and physiological procedures. For example, we measured thresholds to obtain behavioral BMLDs, but due to time constraints, we recorded the FFR at a fixed -10 -dB SNR. Although the study of Clinard et al. (2017) found a correlation between the behavioral NoS π BMLD and the amplitude difference value between the FFR NoSo and NoS π conditions, we note that this correlation was found only in 6/14 participants who had a least a 3-dB behavioral BMLD.

Although the brainstem and midbrain contain neurons that are tuned to ITDs and ILDs, the FFR represents a population response and may not be a robust predictor of the binaural processing required for the behavioral BMLD. Responses measured from cortex may be more closely linked to binaural behavioral performance. Undurraga et al. (2016) found significant correlations between the minimum levels of WB noise required to mask the behavioral response to interaural phase modulations and the amplitude of the cortical response (energy) to these same phase modulations in most of their participants.

Further investigation comparing methods that evaluate responses from different regions may increase understanding of the neural mechanisms underlying the BMLD. For example, cortical peak amplitudes were higher for NoS π compared with NoSo configurations in older individuals (ages 58–83 yr) with progressive supranuclear palsy, a degenerative disease that results in severe atrophy of the brainstem and midbrain among other structures, reducing and/or distorting signals that are sent to cortex (Hughes et al. 2014). These results suggest that the neural processing that contributes to binaural processing may be reflected in measures arising from different levels of the auditory system.

General Discussion

The purpose of this study was to investigate the effects of aging on binaural processing, specifically the BMLD measured perceptually, and to attempt to relate it to changes in electrophysiological potentials generated at the level of the midbrain. Previous research has been mixed about whether behavioral BMLDs can be predicted from electrophysiological recordings. Our approach was to vary stimulus parameters (van de Par and Kohlrausch 1999) and a subject factor, specifically age (Pichora-Fuller and Schneider 1991), to affect the size of the BMLD. We found a wide range of performance in the perceptual BMLDs, especially for the NB NoS π and N π So conditions. This variability in binaural listening tasks is common and has been observed in previous studies (Goupell 2012; Goupell and Barrett 2015). We also noted a wide range of FFR magnitudes in the WB N π So and the NB NoS π conditions. The variability was especially wide in young participants and might be associated with nontest factors such as fatigue. It is possible that repeat testing sessions would reduce this variability, but doubling an 8-h protocol was not feasible for this project. We predicted that a wide range of BMLDs within and across participants would provide a better opportunity to characterize binaural processing in the brainstem/midbrain with the FFR.

Aging effects were found in *experiments 1* and *2*. Behavioral thresholds were significantly higher in older compared with younger listeners for the NoS π and N π So configurations for both BWs, but there were no group differences in thresholds obtained with the NoSo configuration (Fig. 3). The age \times configuration interaction in thresholds resulted in an age-related reduction in BMLDs (Fig. 4) across configurations and BWs, suggesting an overall decrease in the ability to use temporal cues. FFR magnitudes were smaller across phase conditions in the older relative to the younger participants (Fig. 5). Furthermore, the differences in FFR magnitudes between NoS π and N π So configurations for WB and NB BWs were reduced in older participants compared with younger participants (Fig. 7). Despite the range of perceptual performance and FFR magnitudes (Figs. 3 and 6), we did not find correlations among these variables.

Contrasting mechanisms appeared to contribute to smaller perceptual BMLDs and reduced FFR magnitudes in ONH compared with YNH participants. *Experiment 1* revealed age differences were specific to the interaural out-of-phase configurations, suggesting that IPDs were less effective at improving detection of tones in noise in older compared with younger participants. However, *experiment 2* revealed that older participants' responses are degraded across interaural in-phase and out-of-phase configurations. This response degradation may be a factor in the reduced ability to benefit from temporal cues. Because we used a single polarity in our recording, we cannot separate out TFS from envelope components in our responses, but previous studies have shown that aging affects midbrain representation of both TFS and envelope stimulus components (Anderson et al. 2012). Therefore, the older participants likely had reduced representation of the TFS cues that are necessary to benefit from the interaural out-of-phase configurations. Because we found no correlations among behavioral and neural results, we cannot ascertain that this reduced TFS representation was a factor in higher behavioral thresholds for the out-of-phase configurations in older participants compared with younger participants. However, behavioral performance is affected by multiple variables, and perhaps if we had tested cortical BMLDs, we could have supported a claim that TFS representation is an important factor in behavioral performance. In fact, Eddins and Eddins (2018) found an age-related decrease in processing of TFS cues in cortical responses and that the behavioral and cortical BMLDs were highly correlated in both younger and older participants.

Notably, there was a decrease in FFR magnitudes when the 500-Hz tone was presented in noise for dichotic compared with diotic conditions. These findings may be predicted from models of binaural processing. Neurons in medial superior olive and IC can function as coincidence detectors that are tuned to both frequency and ITD, and these neurons respond maximally to specific ITDs (Colburn 1977; Kuwada and Yin 1983; Lane and Delgutte 2005; McAlpine et al. 2001). In the NoSo condition, neurons with preferential responses to zero ITD will increase their firing rates; however, when either the noise or the tone are presented out of phase, or with a non-zero ITD, the firing rate of neurons tuned to a zero ITD decreases.

Animal models have demonstrated that firing rate of single neurons may increase or decrease in the NoS π compared with the NoSo configuration, but the firing rate generally increases in the N π So configuration (Jiang et al. 1997a; Palmer et al.

2000). The direction of change in firing rate for the NoS π configuration in a single neuron appears to depend on that neuron's best delay. The majority of IC neurons respond best to dichotic tones when the tone presented to the contralateral ear leads the tone presented to the ipsilateral ear by 0.2 to 0.4 ms; therefore, a 500-Hz tone with a period of 2 ms will likely have a firing rate at a zero delay that will be close to the best delay (McAlpine et al. 1996). In the S π condition, the 500-Hz tone is presented at 180° interaurally out of phase (an ITD = 1 ms). According to McAlpine et al. (1996), the firing rate decreases for S π compared with So, because a 1-ms delay is close to the worst delay in most neurons. In other words, neurons with a best delay of 1 ms will increase the firing rate for the S π condition, but neurons with a best delay at 1 ms comprise only a small proportion of neurons in IC (Kuwada et al. 1987; Palmer et al. 1990). Therefore, because most neurons in the IC that would contribute to the FFR have best delays of close to zero, we would expect to see a decrease in magnitude in S π compared with So configurations, consistent with our results (Fig. 10).

When comparing NoS π to NoSo, the firing rate appears to increase for neurons with noise best delays at or close to zero (Jiang et al. 1997b). We found a decrease in magnitude in the N π relative to the No configuration, consistent with the suggestion of Palmer et al. (2000) that the N π configuration is less effective at masking the tone because there are fewer neurons tuned to the ITD corresponding to a value of π , and therefore the overall firing rate of neurons responding to the masking noise is decreased.

Because the FFR is a population response, it would be informative to consider the distribution of neurons with best peak delays along a continuum of ITDs across frequency. Joris et al. (2006) obtained single-unit recordings from the IC of cats to broadband noise bursts that varied in ITD. They calculated the ITD that produced the highest firing rate to determine each neuron's best delay and created a graph of this distribution. Most of the best delays for individual neurons were <0.5 ms across the frequency range and at 500 Hz there was a near absence of neurons with best delays of 1 ms, corresponding to π phase (refer to Fig. 2 of Joris et al. 2006). Because we measured population responses to stimuli presented in phase (0-ms ITD, So or No) or out of phase (1-ms ITD, S π or N π), we would expect to see a reduction in magnitude for the S π or N π configurations compared with the So or No configurations, because the overall firing rates would decrease for the π configurations.

Follow-up testing was performed for the NB condition in 10 YNH participants (Fig. 5). This testing used equal stimulus durations and ISIs for the tone and noise, and the results revealed configuration effects that were similar to the WB condition. With the use of equal stimulus durations and ISIs, magnitudes were decreased for the NoS π vs the NoSo configurations, and generally the magnitudes in dichotic configurations were reduced compared with the magnitudes from diotic configurations across tone and noise conditions, consistent with animal models that demonstrate a reduction in neural firing rate to the target stimulus when it is presented in dichotic vs. diotic configurations (McAlpine et al. 1996). The findings obtained when the tone and noise were presented with equal stimulus durations and ISIs differed from the findings obtained when the tone was presented in continuous noise. We are only

able to speculate as to the possible reasons for these differing configuration effects. In the continuous noise condition, the enhanced magnitudes for the NoSo and NoS π conditions relative to the tone only (So) condition may reflect adaptation of inhibition within the critical band of the target tone. This adaptation appears to occur in the auditory system at levels as low as the IC (Borisjuk et al. 2002; Nelson and Young 2010) and thus may also occur in the binaural processing centers of the superior olivary complex. The duration of the noise before the presentation of each stimulus was 100 ms, which should be sufficient to induce adaptation of inhibition (Nelson and Young 2010). A similar finding was not found for the WB condition. The BW of the WB condition exceeded the critical band and may therefore have had less effect on the strength of inhibition in the sidebands adjacent to the target tone.

Conclusion

The behavioral and electrophysiological results revealed an aging effect in both WB and NB conditions, with a reduction in BMLDs and FFR spectral magnitudes. Because we did not find a correlation between behavioral BMLDs and FFR magnitude differences, the aging effect across experiments suggests that independent mechanisms may be resulting in poorer behavioral performance and reduced spectral magnitudes in the older participants. The behavioral decrements in older participants were specific to the dichotic configurations, whereas the decreased spectral magnitudes were noted across all conditions.

Across conditions, we generally found decreased spectral magnitudes in the dichotic compared with diotic configurations, demonstrating binaural processing effects. These results can be best explained when considering of maximal neural firing rates over a range of ITDs (Joris et al. 2006), which would predict a significant decrease in magnitude for stimuli presented with an ITD corresponding to a phase difference of 180°.

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DISCLAIMERS

The content is solely the responsibility of the authors and does not necessarily represent the official views of the National Institutes of Health.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

S.A. and M.J.G. conceived and designed research; S.A., R.E., and J.M. performed experiments; S.A., R.E., J.M., and M.J.G. analyzed data; S.A., R.E., and M.J.G. interpreted results of experiments; S.A., J.M., and M.J.G. prepared figures; S.A. and M.J.G. drafted manuscript; S.A., R.E., J.M., and M.J.G.

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