



How aging impacts the encoding of binaural cues and the perception of auditory space



Ann Clock Eddins^{a, *}, Erol J. Ozmeral^a, David A. Eddins^{a, b}

^a Department of Communication Sciences and Disorders, University of South Florida, USA

^b Department of Chemical and Biomedical Engineering, University of South Florida, USA

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ABSTRACT

Over the years, the effect of aging on auditory function has been investigated in animal models and humans in an effort to characterize age-related changes in both perception and physiology. Here, we review how aging may impact neural encoding and processing of binaural and spatial cues in human listeners with a focus on recent work by the authors as well as others. Age-related declines in monaural temporal processing, as estimated from measures of gap detection and temporal fine structure discrimination, have been associated with poorer performance on binaural tasks that require precise temporal processing. In lateralization and localization tasks, as well as in the detection of signals in noise, marked age-related changes have been demonstrated in both behavioral and electrophysiological measures and have been attributed to declines in neural synchrony and reduced central inhibition with advancing age. Evidence for such mechanisms, however, are influenced by the task (passive vs. attending) and the stimulus paradigm (e.g., static vs. continuous with dynamic change). That is, cortical auditory evoked potentials (CAEP) measured in response to static interaural time differences (ITDs) are larger in older versus younger listeners, consistent with reduced inhibition, while continuous stimuli with dynamic ITD changes lead to smaller responses in older compared to younger adults, suggestive of poorer neural synchrony. Additionally, the distribution of cortical activity is broader and less asymmetric in older than younger adults, consistent with the hemispheric asymmetry reduction in older adults model of cognitive aging. When older listeners attend to selected target locations in the free field, their CAEP components (N1, P2, P3) are again consistently smaller relative to younger listeners, and the reduced asymmetry in the distribution of cortical activity is maintained. As this research matures, proper neural biomarkers for changes in spatial hearing can provide objective evidence of impairment and targets for remediation. Future research should focus on the development and evaluation of effective approaches for remediating these spatial processing deficits associated with aging and hearing loss.

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* Corresponding author. University of South Florida, Department of Communication Sciences and Disorders, 4202 E. Fowler Ave., PCD1017, Tampa, FL, 33620, USA.
E-mail address: aeddins@usf.edu (A.C. Eddins).

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1. Introduction

With the projected increase in the aging population over the coming decades, there are increased expectations for clinicians and others working with older adults to better understand the perceptual changes that occur with age in order to provide effective intervention for treating potential deficits. In relation to hearing, a common complaint of many older adults is the increased difficulty they experience when trying to understand speech in the presence of competing background sounds. In these situations, the listener primarily relies on their binaural system to detect and process the cues necessary to determine the spatial location of the speech as well as cues to help segregate speech from the background competition. Unfortunately, known age-related declines in high-frequency hearing sensitivity (e.g., Allen and Eddins, 2010; Cruickshanks et al., 1998) and in the ability to process important monaural and binaural temporal fine structure and envelope features (Eddins and Eddins, 2017; Gallun et al., 2014; Gordon-Salant and Fitzgibbons, 1999; Grose and Mamo, 2010; Hopkins and Moore, 2009; Ozmeral et al., 2016a) can have a significant impact on the ability of older adults to effectively access and use the cues needed for perception of auditory space and speech understanding in background competition.

Rather than a detailed historical or a basic mechanistic review, the goal of this paper is to provide a contemporaneous overview of how aging influences monaural and binaural cues important for lateralization, localization, and spatial perception while highlighting recent work using cortical auditory evoked response measures to better understand age-related changes in neural mechanisms associated with binaural and spatial processing. With that goal in mind, the sections below begin by highlighting age-related limitations in the processing of monaural cues essential for binaural hearing and spatial processing. This is followed by a discussion of the effects of aging on the processing of simple binaural cues measured using behavioral and electrophysiological methods. Such cues often are best isolated using headphone rather than free-field presentation, and include interaural time difference (ITD), interaural phase difference (IPD), and interaural level difference (ILD) cues. In the context of free-field presentation, age-related changes in sound localization ability as well as sensitivity to and neural coding of changes in spatial location are discussed. Finally, the effects of age and hearing loss on binaural release from masking under headphones and in free-field are considered, including the effects of age on the use of binaural envelope and fine-structure cues.

2. Aging effects on monaural processing important for binaural hearing

When considering the process by which sound is perceived in a natural environment, one typically thinks about mechanisms involved in binaural as opposed to monaural processing. However, a number of studies have shown that monaural sensitivity to brief temporal gaps, temporal fine structure (TFS; i.e., rapid amplitude fluctuations over time), and temporal envelope (i.e., slow amplitude fluctuations over time) of the acoustic stimulus plays an

important role in binaural function (Dobrevá et al., 2011; Eddins and Eddins, 2017; Fullgrabe, 2013; Gallun et al., 2014; Grose and Mamo, 2010; Ross et al., 2007). Importantly, deficits in such monaural tasks occur with both advancing age and hearing loss, and thus should be considered when evaluating binaural and spatial perception in older adults.

The auditory system is known to function with great sensitivity, speed and temporal precision from the auditory periphery through the ascending central auditory pathway. With advancing age, not only is there reduced sensitivity (Allen and Eddins, 2010; Cruickshanks et al., 1998; Gates et al., 1990), but precise temporal coding deteriorates over time and is one major factor thought to underlie age-related declines across a number of perceptual measures, including speech perception (Fullgrabe et al., 2014; Gordon-Salant and Fitzgibbons, 1999; Pichora-Fuller et al., 2007; Snell et al., 2002). To estimate changes in temporal envelope coding with age, one of the most common perceptual measures has been temporal gap detection (Humes et al., 2012). This task measures the shortest detectable silent interval between two stimulus markers, typically noise or tones. Monaural temporal gap detection thresholds (TGDTs) for broadband noise in young, normal-hearing listeners is typically between 2 and 3 ms (Eddins and Green, 1995; Green, 1971). Studies of gap detection in older listeners have shown reduced performance with increasing age (Lister and Roberts, 2005; Moore et al., 1992; Roberts and Lister, 2004); however, concomitant changes in hearing sensitivity often make it difficult to determine whether poorer temporal gap detection is due to age, reduced sensitivity, or a combination of both. In a systematic review by Humes and colleagues (Humes et al., 2012), it was reported that nine out of 12 studies included in the review reported significant effects of age on TGDTs, consistent with other recent studies (John et al., 2012; Palmer and Musiek, 2014). Gap detection measures were evaluated recently in a large cross-sectional study of aging and temporal acuity (Ozmeral et al., 2016a). TGDTs were measured in 1071 listeners (ages 18–98 years) for Gaussian noise bursts that were low-pass filtered at either 1 kHz or 4 kHz. Starting from the youngest through about 65 years of age, TGDTs for the 1-kHz condition increased progressively at a rate of 1.05 ms per decade (15% change per decade relative to thresholds at 18 years) and at a more accelerated rate of 1.15 ms per decade beyond about 65 years of age (15% change per decade relative to thresholds at 65 years; Fig. 1). Results from the 4-kHz condition showed a slightly more rapid increase beyond about 67 years of age (1.23 ms or 29% per decade). When controlling for audibility and limiting the analyses to individuals with clinically normal hearing sensitivity ($n = 434$), age remained a significant predictor of gap detection threshold, where TGDTs increased roughly 16% and 24% per decade for the 1- and 4-kHz conditions, respectively. Further, a significant sex difference was observed across the full and normal-hearing datasets such that TGDTs were, on average, shorter for males (6.8 ms) than for females (10.3 ms).

In addition to gap detection, the influence of age has been evaluated on other monaural measures thought to reflect temporal fine structure processing. For example, the detection of low-rate frequency modulation imposed on tonal carriers has been used due to its dependence on phase-locking to the temporal fine

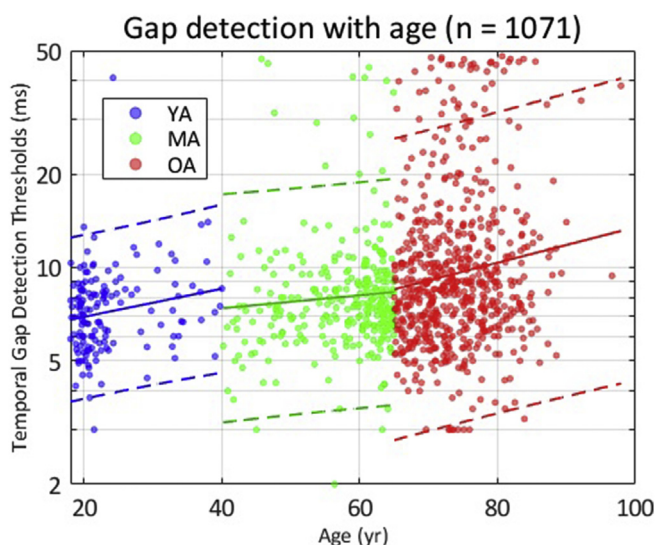


Fig. 1. Temporal gap detection thresholds (TGDT; ms) in a 1-kHz condition for 1071 individuals spanning ages of 18–98 years. A lognormal function was fitted for each of 3 broad age groups (18–40, 40–64, 65+ years). Mean gap detection thresholds for the young, middle and older age groups were 7.52, 8.74, and 11.31 ms, respectively. The 95% confidence intervals were computed for each group and are shown by the dashed lines. (Adapted from Ozmeral, Eddins, Frisina and Eddins, 2016a).

structure of the carrier frequency (Buss et al., 2004; Grose and Mamo, 2012b; Moore and Sek, 1996; Strelcyk and Dau, 2009). In such tasks, listeners are detecting the presence of low rate (e.g., 2 Hz) frequency modulation of a tonal carrier (e.g., 500–1500 Hz). Results from these monaural measures have indicated reduced performance in middle age to older adults with sensorineural hearing loss as compared to normal-hearing control groups (Buss et al., 2004; Grose and Mamo, 2012b; Strelcyk and Dau, 2009). Although aging was not evaluated independent of hearing loss in these investigations, one would hypothesize that reduced temporal coding with age would likely lead to poorer performance in such monaural TFS measures as well.

In addition to monaural temporal processing, monaural spectral processing provides essential support for normal and accurate spatial hearing. Outer ear anatomy, including the pinna and ear canal, as well as other head-related characteristics, collectively form a network of filtering processes that shape the spectrum of the input signal in a manner that is dependent on sound source position. This position-dependent filtering produces spectral cues unique to the individual listener that are important for localizing sounds in the free field, particularly in the vertical plane (Butler and Humanski, 1992; Middlebrooks, 1992; Middlebrooks et al., 1989; Middlebrooks et al., 1999a,b; Rogers and Butler, 1992; Shaw, 1966). While the physical properties that form the spectral cues are not considered age dependent, the availability of the cues and the ability to effectively process them may be. These spectral cues span most of the usable auditory range, though the most position-dependent information is above 5–6 kHz. Because age-related changes in audibility begin at higher frequencies and progressively encroach lower and lower frequencies, the availability of such spectral cues declines with age simply due to reduced stimulus audibility. Indeed, earlier studies attributed such declines in high-frequency audibility to the reduction of the availability of such “pinna” spectral cues, leading to poorer vertical localization performance with advancing age (Abel and Hay, 1996; Rakerd et al., 1998). A second potential limitation would be age-related declines in the ability to use spectral cues that are audible. Systematic investigation of the effects of age and hearing loss on spectral shape

perception, however, indicates that age *per se* does not impair the ability to detect changes in spectral shape such as those used in spatial hearing. Specifically, the detection of sinusoidal spectral modulation was measured as a function of spectral modulation frequency (in cycles per octave) for four groups of listeners including groups of young and older listeners with normal pure tone thresholds, and groups of older listeners with mild or moderate sensorineural hearing loss. There was a significant effect of hearing loss on the resulting spectral modulation transfer functions but no significant effect of age and no significant interaction (Eddins et al., 2006). Thus, the spectral cues known to be important for spatial hearing in the vertical plane may be limited in their availability due to loss of audibility with age but when sufficiently audible, aging does not appear to limit the ability to use such cues.

3. Binaural processing of interaural time, phase, and level differences

The perceived spatial location of sounds, whether lateralized within the head or localized in the sound field, primarily relies on the ability of the auditory system to compare sounds arriving at the two ears using interaural time difference (ITD) and interaural intensity or level difference (IID, ILD) cues (Rayleigh, 1907; Wightman and Kistler, 1992). These cues combine with monaural pinna and head-related spectral cues when localizing sounds in the free field (Middlebrooks, 1992; Middlebrooks and Green, 1991). For ongoing and periodic sounds (e.g., tones), comparing interaural phase differences (IPDs) can also provide lateralization cues for stimuli up to about 1500 Hz in humans (Zwislocki and Feldman, 1956). If, however, a higher-frequency stimulus is amplitude modulated by a low-frequency tone, interaural timing differences can be introduced in the temporal envelope to provide cues for lateralization (Bernstein and Trahiotis, 2002; Grose and Mamo, 2010; Henning, 1974; McFadden and Pasanen, 1976).

3.1. Aging effects on behavioral measures of ITD, IPD, and ILD processing

The literature on ITD, IPD and ILD sensitivity in young and older listeners, as well as in individuals with hearing loss, is ever expanding. ITD sensitivity measures, in particular, are useful metrics for examining age-related changes in binaural temporal coding within the auditory periphery and central pathway. Perhaps not surprising, several studies using psychoacoustic measures of ITD processing have shown age-related declines even when controlling for the confounding effects of age-related hearing loss or presbycusis (Babkoff et al., 2002; Strouse et al., 1998). For instance, Strouse et al., 1998 evaluated aging effects on auditory temporal processing using a battery of tests, including ITD sensitivity for a 100-Hz pulse train, in younger (mean age = 26.1 years) and older (mean age = 70.9 years) adults with normal hearing (≤ 20 dB HL, 250–6000 Hz) that were matched for sex and hearing sensitivity. For ITD thresholds measured across three sensation levels, older listeners required about twice as long of an ITD on average as younger listeners in order to achieve the same performance. When stimulus level (dB SL) was decreased, ITD discrimination for older adults was impacted to a greater extent relative to younger adults.

Similar to the observed age-related reductions in ITD processing, aging also imposes frequency limits on processing of IPD cues due to declines in phase locking and fine structure coding with age. Ross et al. (2007) measured the ability to detect an IPD change (180° phase inversion) for 40-Hz, sinusoidal amplitude-modulated (SAM) tonal carriers (375–1500 Hz) using both psychophysical and magnetoencephalographic (MEG) techniques in young (mean = 26.8 years), middle-age (mean = 50.8 years), and older

(mean = 71.4 years) adults with normal or near-normal hearing (<30 dB HL, 250–2000 Hz). They showed that the highest frequency for which a single, fixed IPD change could be detected in both behavioral and cortical evoked response measures decreased with increasing age; 1225 Hz for young listeners, 940 Hz for middle-age listeners, and 760 Hz for older listeners. When quantified across listeners from all age groups, there was a 10% decrease per decade in the frequency limit for detecting an IPD change, where the decline began in middle age. Similar age-effects on IPD processing were reported by [Grose and Mamo \(2010\)](#) for young, middle-age and older adults. In one experiment, they measured the highest frequency at which a 5-Hz SAM tone with a dynamic phase inversion on alternating periods of modulation could be discriminated from a diotic SAM tone standard. They reported a similar age-related decline in the upper frequency limit for detecting an IPD change that began in middle age (~47.5 years), although with less individual variability across participants as compared to [Ross et al. \(2007\)](#). [Grose and Mamo \(2010\)](#) also measured the just-noticeable IPD for pairs of tone pulses over a range of fixed frequencies (250–1500 Hz) and showed that, although the older group had the poorest IPD thresholds overall, the middle-age listeners were less sensitive than younger listeners to IPDs at all but the lowest frequencies (250, 500 Hz). Again, these results are consistent with declines in binaural temporal fine structure processing that is evident in middle and older age adults with clinically normal hearing (≤ 2 kHz).

There are far fewer investigations of ILD sensitivity in older adults than those of ITD or IPD. Both [Herman et al. \(1977\)](#) and [Babkoff et al. \(2002\)](#) evaluated ITD and ILD sensitivity in older adults, and while their results indicated poorer ITD sensitivity with increasing age, neither study reported an age effect on ILD processing. One possible confound in testing ILD sensitivity is that listeners may use a strategy based on cues from monaural intensity changes. That is, when the intensity is decreased in one ear and increased in the other ear, the listener may be tracking the level changes in one ear only and making decisions based on that one ear alone. Although it is challenging to isolate such a strategy, this has not been investigated with regard to aging effects but may be useful to do so in future studies. Likewise, additional studies are needed to better understand potential effects of aging on IID sensitivity in general.

3.2. Aging effects on electrophysiological measures of ITD, IPD, and ILD processing

The challenge of understanding why older adults may or may not have difficulty making use of binaural cues has led many to evaluate potential changes in the underlying physiological correlates of binaural and spatial processing. As a result, there is an extensive literature based on both animal and human data that describes the putative mechanisms by which interaural and relevant monaural cues are encoded from the brainstem to auditory cortex ([Grothe et al., 2010](#); [Jeffress, 1948](#); [Konishi, 2003](#); [Magezi and Krumbholz, 2010](#); [McLaughlin et al., 2016](#); [Middlebrooks et al., 1994](#); [Salminen et al., 2012](#)). Traditionally, it was assumed that binaural cues, such as ITDs, were coded by a population of neurons organized topographically within auditory nuclei and cortex and each tuned to a narrow range of ITDs ([Jeffress, 1948](#)). Whereas this type of coding model may be applicable to owls ([Carr and Konishi, 1990](#); [Konishi, 2003](#)), more recent research in mammals points toward an opponent-channel model in which neural populations are more broadly tuned to the left or right hemifield, and sound source location is inferred by the relative balance of activity between the two opposing neural channels ([Briley et al., 2013](#); [Derey et al., 2016](#); [Grothe et al., 2010](#); [Magezi and Krumbholz, 2010](#); [McAlpine and Grothe, 2003](#); [Phillips, 2008](#); [Stecker et al., 2005](#)). To

evaluate this model in humans, [Magezi and Krumbholz, 2010](#) used electroencephalography (EEG) to measure cortical event-related potentials to shifts in ITD in which the stimuli were perceived as moving either outward (away from midline) or inward (toward midline). Based on an opponent-channel (hemifield) model, an outward shift toward the left hemifield, for example, would produce a larger response relative to an inward shift due to greater contribution from the left channel. In contrast, a topographic model of narrowly tuned neurons would predict responses of similar magnitude regardless of the direction of change, either inward or outward. Indeed, [Magezi and Krumbholz, 2010](#) showed that coding of ITD-change sensitivity in a group of young normal-hearing listeners was consistent with an opponent-channel model and that the distribution of responses in each hemisphere were dominated by ITDs corresponding to the contralateral hemifield.

To evaluate whether aging alters such an opponent-channel coding process for ITDs, it is important to consider potential age-related changes in central auditory function that might influence neural responses to ITDs. For instance, the progressive decline in auditory sensitivity that typically has been attributed to peripheral deafferentation has been linked to a compensatory downregulation of inhibition at multiple levels in the central pathway of aging animal models (for review, see [Casparly et al., 2008](#)). In humans, reduced inhibition at the level of the cortex has been inferred from changes in evoked response amplitudes (e.g., P1, N1, P2), where older adults often have larger amplitudes compared to younger adults in response to similar stimuli ([Grose and Mamo, 2012a](#); [Harkrider et al., 2005](#)). In addition to changes in inhibition, aging also has been associated with declines in neural synchrony or temporal coding precision ([Anderson et al., 2012](#); [Grose and Mamo, 2010, 2012a](#)), which would clearly have implications for neural processing of ITDs.

We recently investigated aging effects on opponent-channel coding for ITDs with the added question of whether potential changes might reflect mechanisms associated with reduced inhibition, reduced temporal synchrony or both. Cortical auditory evoked responses were recorded in a passive paradigm for a series of fixed or static ITDs (−500, −250, 0, +250, +500 μ s) using low-frequency narrowband noises (500–750 Hz, 400-ms, 10-ms rise/fall window) presented under headphones at 80 dB SPL at a rate of one per two seconds (ISI 1.6 s). Participants were ten young (mean = 24.9 years) and ten older (mean = 70 years) listeners with clinically normal hearing (≤ 25 dBHL, 250–4000 Hz). The EEG data from 64-channels were preprocessed (filtered, eye blink artifacts detected/rejected, epoched, and averaged), and then global field power (GFP) was computed to estimate the magnitude of the responses across electrodes and grand-averaged for each group. [Fig. 2](#) shows the GFP mean (dashed lines) and standard deviation (shaded regions) for the young (blue) and older (red) listeners across the five ITDs spanning left-leading (L500) and right-leading (R500) conditions.

To evaluate effects of ITD condition, age group and evoked response component (P1, N1, P2), an analysis of variance was completed. There was a significant main effect of age group ($F[1,18]=8.42$, $p<0.01$), consistent with the larger responses consistently observed for the older group relative to the younger group. There also was a significant main effect of response component ($F[2, 36]=11.2$, $p<0.001$) corresponding to the significantly larger N1 than P1 magnitude ($p=0.008$) and P2 ($p=0.001$). There were no significant differences in GFP across ITD conditions and no significant interactions ($p>0.05$). Based on putative underlying mechanisms, these results are consistent with reduced inhibition in the central auditory pathway with increasing age, thus leading to larger responses in older versus younger listeners. The results, however, are not easily interpreted in the context of an opponent channel model.

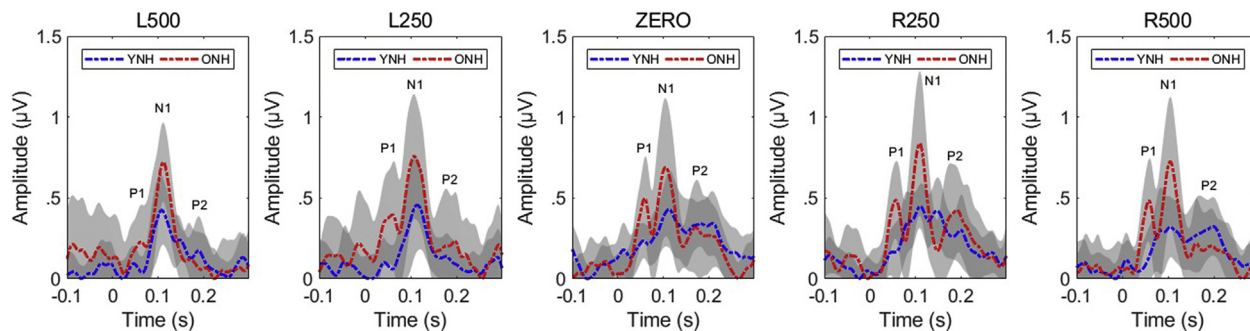


Fig. 2. Average global field power (GFP) computed for younger ($n = 10$, blue) and older ($n = 10$, red) normal-hearing listeners in each of 5 ITD conditions. Mean GFPs are shown by dashed lines and standard deviations are shaded around the mean. Cortical evoked response components (P1, N1, P2) are indicated in each panel. Time (s) is relative to the onset of the stimulus.

To better assess the opponent channel model, an EEG paradigm similar to [Magezi and Krumbholz, 2010](#) was employed to measure aging effects on cortical evoked responses (P1, N1, P2) to dynamic inward and outward changes in ITD ([Ozmeral et al., 2016b](#)). The stimuli were narrowband noises (NBN; 500–750 Hz), where an adapter (~1600 ms) was one of five ITDs (−500, −250, 0, +250, +500 μ s) and was followed immediately by a NBN probe stimulus (~400 ms) at another ITD. The evoked response elicited by the change in ITD between adapter and probe was analyzed with regard to the direction of the shift, either inward (toward) or outward (away) relative to midline. The results showed that both younger normal-hearing listeners (mean = 24.9 years) and older normal-hearing listeners (mean = 70.0 years) had significantly larger magnitude responses for N1 and N1–P2 for outward versus inward shifts, consistent with the opponent channel model and previous ITD studies ([Magezi and Krumbholz, 2010](#); [Salminen et al., 2010, 2012](#)). In contrast to the results described above for a static ITD (see [Fig. 2](#)), the dynamic shift in ITD lead to significantly longer latencies for N1 and P2 for older versus younger listeners, and older listeners tended to have smaller magnitude responses relative to younger, although the difference did not reach statistical significance (see [Figure 4, Ozmeral et al., 2016b](#)). Taken together, data from both static and dynamic ITD shifts demonstrate age-related changes in cortical responses consistent with both reduced central inhibition and reduced neural synchrony, similar to other investigations of binaural temporal processing in older adults ([Briley and Summerfield, 2014](#); [Eddins and Eddins, 2017](#); [Grose and Mamo, 2010, 2012a](#); [Ross et al., 2007](#)). An important and novel result from this study was the observation of an altered distribution of cortical activity in the young versus older group. Specifically, younger listeners showed an asymmetric distribution of cortical activity, particularly at the time interval corresponding to P1, in which inward shifts were lateralized more to the left hemisphere and outward shifts were lateralized more to the right hemisphere. Older adults, in contrast, showed a more balanced distribution of activity during ITD processing (see [Figure 7, Ozmeral et al., 2016b](#)). This reduced asymmetry relative to younger listeners, in the context of binaural hearing, is consistent with the hemispheric asymmetry reduction in older adults (HAR-OLD) model of cognitive aging ([Cabeza, 2002](#)) but in this case extended to sensory (auditory) processing.

4. Binaural processing of spatial cues in the free-field

4.1. Aging effects on behavioral measures of sound localization

Free-field sound localization relies on both binaural and monaural cues to accurately identify a source location in both the vertical and horizontal planes. Whereas ITDs and ILDs are the

dominant cues for horizontal sound localization, high-frequency monaural cues contribute significantly to vertical sound localization as well as to resolving front-back errors ([Carlile et al., 1999](#); [Middlebrooks, 1992](#)). Localization of wideband stimuli is often characterized by overshoot in the horizontal plane ([Choisel and Zimmer, 2003](#); [Seeber, 2002](#); [Wightman and Kistler, 1989](#)) and undershoot in the vertical plane ([Carlile et al., 1999](#); [Carlile et al. 1997](#); [King and Oldfield 1997](#)), with greater errors associated with narrower spectra that limit the favored frequency ranges for dominant cues. Middle-aged and older listeners show increased errors relative to younger controls in both planes, presumably due to a combination of declines in peripheral and central mechanisms ([Dobrevá et al., 2011](#)). As described above, poor ITD coding is a hallmark of presbycusis, and indeed, older and even middle-aged listeners are susceptible to more errors and greater overshoot in horizontal localization than younger adults. In the vertical plane, listeners who exhibit signs of peripheral presbycusis (i.e., gradually sloping high-frequency hearing loss) are less precise in localization tasks and have greater undershoot than younger listeners ([Dobrevá et al., 2011](#)).

4.2. Aging effects on electrophysiological measures of spatial processing

To extend the investigation of age-related changes in electrophysiological measures of ITD processing to the free field, we used an EEG paradigm comparable to [Briley and Summerfield \(2014\)](#) to evaluate cortical responses to abrupt changes in sound location of a low-frequency NBN (500–750 Hz, 1600 ms, 80 dB SPL) for both younger ($n = 10$, mean = 22.9 years) and older listeners ($n = 8$, mean = 68.1 years). The stimuli were presented continuously (no interstimulus interval) and randomly from five speaker locations spanning -60° to $+60^\circ$ with 30° resolution in the front horizontal plane positioned 1 m from listener. Evoked responses were triggered and recorded relative to the onset of the stimulus at a given location. Similar to [Ozmeral et al. \(2016b\)](#), we computed the GFPs based on the direction of stimuli as they moved either inward or outward relative to midline when presented in a passive listening condition.

[Fig. 3](#) (left panel) shows our previous data for ITD directional shifts in a passive condition under headphones (from [Ozmeral et al., 2016b](#)) that indicated significantly larger responses for combined N1 and P2 GFP magnitudes for outward versus inward shifts for both younger and older listeners. This was supported by an ANOVA with age and direction as factors that showed a significant effect of direction [$F(1, 16) = 5.18, p = 0.037$] but not age, and no significant interaction. [Fig. 3](#) (right panel) shows similar results for spatial shifts in the free-field, where responses were larger for

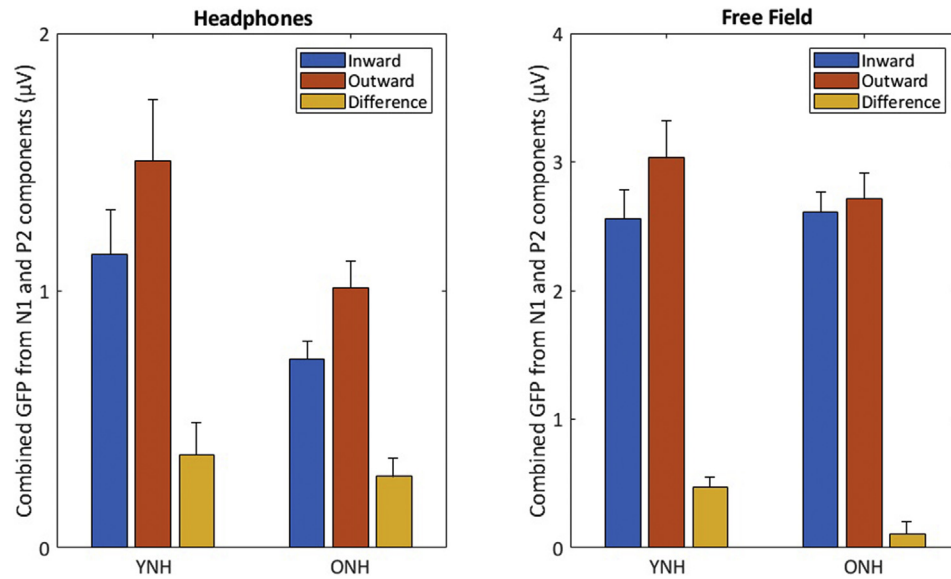


Fig. 3. Average combined global field potential (GFP) for N1 and P2 components of the evoked response to changes in a lateralized narrowband noise under headphones (left panel; adapted from Ozmeral, Eddins and Eddins, 2016b) or free-field spatial location shift (right panel; error bars indicate 1 standard error of the mean). Responses to shifts in the outward direction were significantly larger than for inward shifts as would be predicted by an opponent-channel model of spatial coding; however, only in the free field was an interaction found between age and direction of the spatial shift.

outward versus inward shifts for both age groups, based on an ANOVA with age and direction as factors ($F[1,16] = 23.6, p < .001$). Unlike for ITD shifts under headphones, however, there was a significant interaction between shift direction and age group ($F[1,16] = 9.2, p < .01$), corresponding to the disproportionately larger amplitudes for the outward shifts in younger listeners compared to older listeners despite similar amplitudes between groups for the inward shifts. Although the free-field processing was likely dominated by ITD cues for these low-frequency NBN test stimuli, the observed interaction indicates that additional monaural (i.e., head-related spectral shaping) and binaural (i.e., ILD) cues available in the free-field condition affected the listening groups differentially.

In addition to the passive free-field condition, young and older participants also were tested in two spatial attention conditions in which they were instructed to attend to a left target location (-30°) or right target location ($+30^\circ$) and press a button when the sound was heard at that location. The same NBN stimuli (500–750 Hz, 1600 ms, 80 dB SPL) were presented continuously in random order to the same five speaker locations (-60° to $+60^\circ$). Again, the evoked responses were triggered and recorded relative to the onset of the stimulus at a given location. When examining grand average responses across groups at a single electrode (i.e., Cz), as is often common practice in clinical settings and with some research groups, the results showed prominent N1 and P2 components as well as an attention-related P3 component for stimuli presented at the attended target locations for young listeners. For older listeners, however, only N1 and P2 but no prominent P3 components were observed at this single electrode. Different results were obtained when the grand average GFP was computed for each group by condition and spatial location (see Fig. 4). With this analysis, both young (top row) and older (bottom row) groups showed more robust N1 and P2 response components at all locations during the attention conditions (red and blue lines) relative to the passive condition (black lines). In addition, GFP responses at the two target locations show the additional P3 component for both young and older groups when participants attended either left (-30° , left panel) or right ($+30^\circ$, right panel), respectively (see Fig. 5). A repeated measures analysis of variance was completed to evaluate

age group and condition effects on P3 magnitudes at the two target locations and showed an effect of condition ($F[2,30] = 31.9, p < .001$) and interactions between condition and group ($F[2,30] = 3.93, p = .03$) and between condition and location ($F[2,30] = 25.9, p < .001$). The latter interaction is explained simply by the increased P3 response in the Attend Left condition at -30° and complementary increased P3 response in the Attend Right condition at $+30^\circ$. The former interaction appears to be driven by greater responses in the active attention conditions for the younger relative to the older normal-hearing group. These data indicate that there is an overall reduction to evoked responses in older listeners when actively attending to spatial location, which may be driven by reduced temporal synchrony.

5. Binaural and spatial release from masking

5.1. Aging effects on the binaural masking level difference (BMLD)

Binaural cues also provide valuable information that can aid our perception of target stimuli in the presence of competing backgrounds. One well-known paradigm for demonstrating this effect is the binaural masking level difference (BMLD), in which the detection threshold for a signal presented simultaneously in noise to both ears improves by altering the phase of either the signal or noise at the two ears. This interaural phase-dependent threshold reduction is referred to as a masking release. The most common BMLD paradigm includes a reference condition in which a tonal signal (So) and noise (No) are presented diotically (in-phase) at the two ears (i.e., NoSo) and a comparison condition in which the noise remains diotic but the tonal signal is 180° out-of-phase at the two ears (i.e., NoS π). The magnitude of the masking release (in dB) is simply the difference in detection threshold between the reference and comparison conditions. The release from masking in the comparison condition has been attributed to our ability to perceive subtle changes in the interaural cross-correlation of the signals between ears (e.g., Bernstein and Trahiotis, 2002).

Over the past couple of decades, there have been a number of investigations of age-related changes in behavioral measures of the

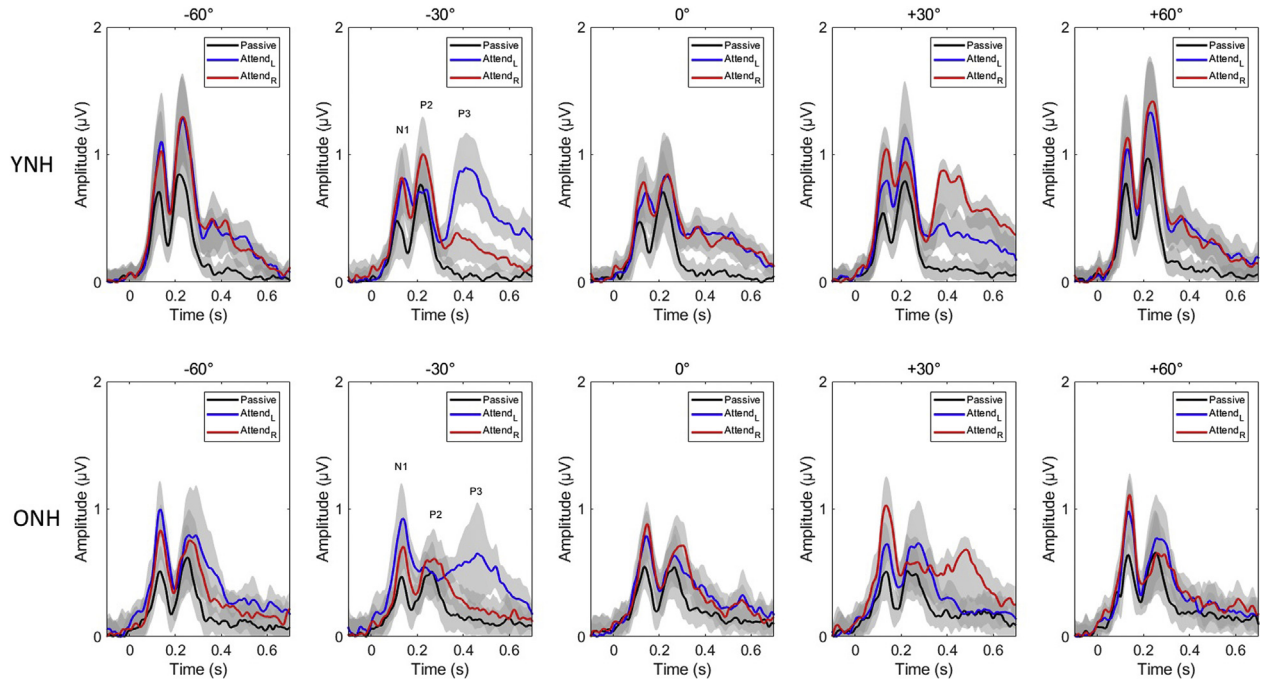


Fig. 4. Mean GFP (dashed lines) and standard deviations (shaded area) were computed for younger ($n = 10$, top row) and older ($n = 8$, bottom row) normal-hearing listeners in three localization conditions (Passive, Attend Left [-30°], and Attend Right [$+30^\circ$]) and from five speaker locations. Cortical evoked response components (P1, N1, P2, P3) are indicated in the second panels from the left. Time (s) is relative to the onset of the stimulus at each respective location.

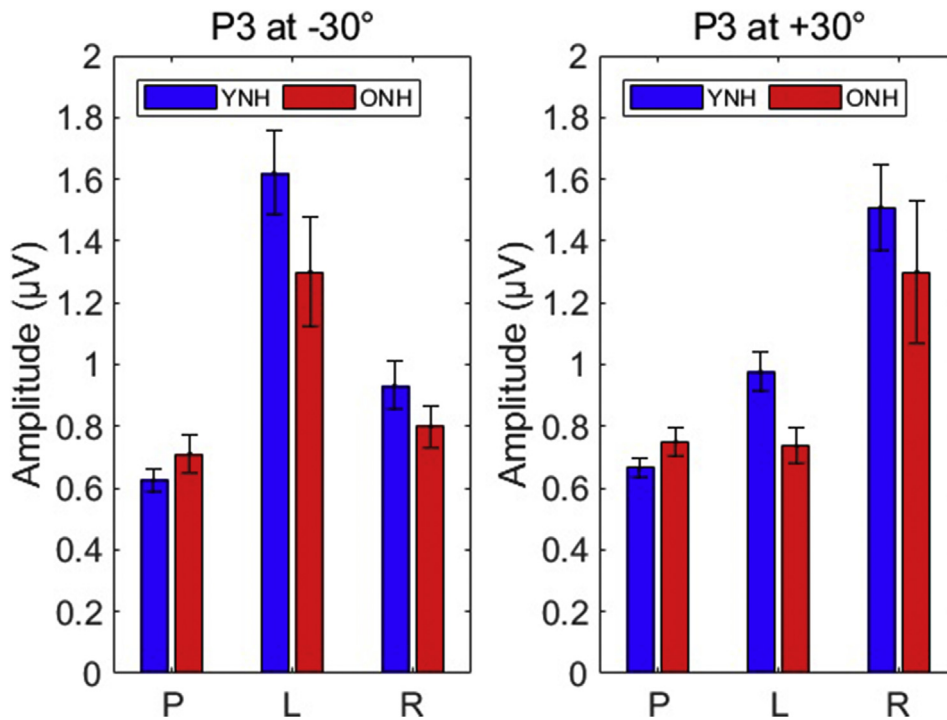


Fig. 5. Mean amplitudes (\pm standard error of the mean) of the GFP of the P3 response in YNH listeners ($n = 10$; blue bars) and ONH listeners ($n = 8$; red bars). Each magnitude value was extracted for the Passive (P), Attend Left (L) and Attend Right (R) conditions for the -30° (left panel) and $+30^\circ$ (right panel) locations.

BMLD (Dubno et al., 2008; Grose et al., 1994; Pichora-Fuller and Schneider, 1991; Strouse et al., 1998). It is clear from these studies that older listeners tend to have less release from masking than younger listeners, but the origins of that reduction are not well understood. To better understand processes that may lead to age-

related declines in the binaural masking release, Eddins and Eddins, 2017 used behavioral and cortical auditory evoked potential (CAEP) threshold measures in young and older listeners with and without hearing loss. They used a unique stimulus set designed to assess potential age-related changes in temporal fine structure

and temporal envelope coding. To estimate contributions of temporal fine structure coding, low (500 Hz) and high (4000 Hz) frequency stimuli were used, as the natural decline in phase-locking was expected to limit fine structure coding for high-frequency stimuli but less so for low-frequency stimuli. Likewise, contributions of temporal envelope coding was evaluated by manipulating the envelope of narrowband (50-Hz wide) noise maskers centered on the tones, where narrowband Gaussian noise (GN) maskers had robust envelope cues and low-noise noise (LNN) maskers had minimized envelopes. The results showed that older listeners did indeed have smaller magnitude BMLDs for both behavioral and CAEP measures, and that the greatest age-related effects were for low-frequency tones in both GN and LNN maskers. This was attributed to poorer temporal fine structure processing with age. In contrast, no significant age effects in the BMLD were observed for high frequency stimuli, for which any masking release would be attributed to temporal envelope processing. The behavioral results, shown in Fig. 6 (data sets 1 and 2), are consistent with several previous studies of BMLD (Fig. 6, data sets 3 to 6) as well as other studies of binaural hearing that have shown declines in temporal fine structure coding with increasing age (Gallun et al., 2014; Grose and Mamo, 2010; Papesh et al., 2017; Ross et al., 2007). Importantly, there was a strong correlation between the BMLDs computed from behavioral and CAEP data across all conditions and for listeners of all ages (see Figure 6, Eddins and Eddins, 2017), indicating that CAEP measures of the BMLD may be a viable biomarker of binaural temporal processing.

5.2. Aging effects on the spatial release from masking for speech

The ability to locate and selectively attend to target sounds of interest (e.g., non-speech or speech) in the free field can be significantly impacted when additional competing (i.e., masking) sounds are present. This situation is typical of the “cocktail party” problem in which listeners have to ignore or suppress the competing maskers in order to effectively process and segregate the target sound. While humans are remarkably well equipped to deal with this problem, the ability to do so declines with age. Making use of interaural (ITD, IID) and monaural spectral cues can certainly aid the listener in segregating the source from the masker,

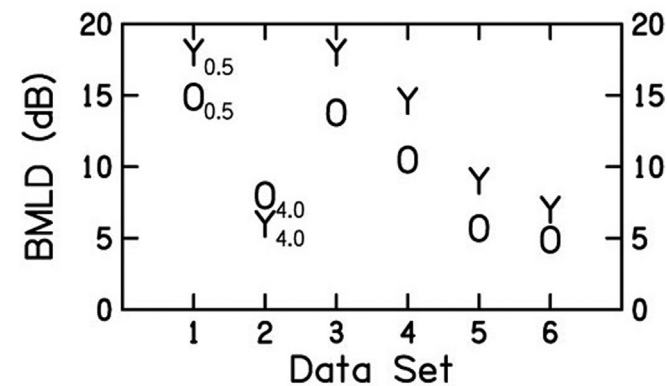


Fig. 6. Binaural masking level differences (BMLD) averaged for young (Y) and older (O) listeners in continuous maskers. Data sets 1, 2, 3 and 4 are for tonal signals and data sets 5 and 6 are for speech signals. Data sets 1 and 2 are from Eddins and Eddins (2017) for 500 and 4000 Hz pure-tones presented in 50-Hz wide Gaussian noise maskers centered on the tone frequency. Data set 3 is from Grose et al. (1994) for a 500-Hz pure tone in 100-Hz wide noise centered on 500 Hz. Data set 4 is from Pichora-Fuller and Schneider (1991) for a 500-Hz pure tone and noise band from 100 to 5000 Hz. Data set 5 is from Grose et al. (1994) and set 6 from Strouse et al. (1998) where both studies used spondaic words in speech-shaped noise maskers. Adapted from Eddins and Hall (2010).

but a perceptual advantage occurs when the maskers are spatially separated from the target (Best et al., 2005; Brungart and Simpson, 2007; Hawley et al., 2004). With hearing loss or advancing age, however, listeners may not be able to obtain the same benefit from spatial separation as younger, normal-hearing listeners. For example, Glyde et al. (2013) investigated the effects of aging, hearing loss and cognitive ability on spatial processing of speech using the Listening in Spatialized Noise-Sentences test (LiSN-S). The test uses an adaptive paradigm to measure speech reception thresholds for target sentences presented directly in front of the listener (0°) simultaneously with distracter speech (masker) that has the same or different voice (i.e., fundamental frequency) as that of the target. Speech reception thresholds are measured in four spatial conditions; same voice with target and distracter co-located (0°), same voice with distracter at $\pm 90^\circ$, different voices co-located (0°), and different voices at $\pm 90^\circ$. These various conditions allow one to evaluate the advantage of speech perception in background competition relative to the talker (same vs. different voices), spatial location (co-located vs. spatially separated), and total advantage (different voices, spatially separated). In addition to other measures, they tested performance on the LiSN-S for 80 participants (range 7–89 years, mean = 50.17 years, SD = 26.33 years), where about 30% had clinically normal hearing and the remainder had hearing loss with about 44% reporting use of amplification (Glyde et al., 2013). The stimuli were presented under headphones using average head-related transfer functions to create the spatialized stimuli, and gain was compensated for those with hearing loss. The results showed that hearing loss was the primary factor affecting the amount of improvement achieved from the spatial advantage, whereas age and cognitive ability showed no significant correlation with spatial processing ability.

An alternative approach used by Gallun et al. (2013) was to measure the spatial advantage for target speech spatially segregated from competing speech in both a free-field and virtual space paradigm. In their speech spatial release task, listeners are presented with three simultaneous utterances from the Coordinate Response Measure (CRM; Bolia et al., 2000) and are instructed to attend to one of the sentences identified by a specific call-sign (e.g., Charlie). The target utterance is presented from a speaker located directly in front of the listener (0°), and the two competing utterances are presented from either the same speaker (i.e., co-located at 0°), or from spatially separated speakers ($\pm 15^\circ$, $\pm 30^\circ$, or $\pm 45^\circ$). Thresholds for the target utterance are measured adaptively and reported as target-to-masker ratios for conditions in which the target and maskers are of the same sex (e.g., male/male) or different sex (e.g., male/female). To investigate the effects of age and hearing loss on spatial release from masking (SRM), Gallun et al. measured spatial release in an anechoic environment and in virtual space using headphones, where CRM stimuli were convolved with average head-related impulse responses (HRIR) to provide spatialization (Gallun et al., 2013). In a large group of listeners ($n = 52$), ranging in age from 19 to 76 years (mean = 45.3 years, SD = 17 years), they showed that age and hearing loss were independent factors contributing significantly to reduced spatial release from masking in both anechoic and virtual-space environments. In fact, age accounted for almost twice the amount variance as hearing loss when equating for audibility of the stimuli across listeners and ears. In addition, the fact that comparable results were achieved with their implementation of virtual space supports the potential for its use in other research and clinical environments. The studies by Glyde et al. (2013) and Gallun et al. (2013) arrived at different conclusions regarding the influence of age despite their use of large numbers of subjects spanning a wide range of age and hearing loss. Both used statistical methods rather than disparate subject groups in their efforts to address the potential impacts of age and hearing

loss on spatial release from masking. Perhaps future research designed to separately evaluate the effects of age and hearing loss via unique subject groups will be able to better address and separate effects of age from the effects hearing loss. Practically, however, typical aging is accompanied by loss of audibility and both studies indicated that advancing age combined with hearing loss likely leads to reduced spatial release from masking and thus contributes to the common complaint of difficulty understanding speech in complex listening environments.

In a recent electrophysiological investigation, Papesh et al. (2017) sought to identify neural indices that may provide an objective measure of the effects of aging and hearing loss on the ability to benefit from SRM. They measured cortical responses to a 180° interaural phase change embedded in the temporal center of amplitude-modulated (100%, 10 Hz) carrier tones (750, 1000, 1250 Hz) in groups of young (mean = 26.5 years) and middle-age (mean = 51.1 years) normal-hearing adults and groups of middle-age (60.8 years) and older (mean = 71.4 years) adults with hearing loss. The older hearing-impaired group had significantly greater pure-tone average (500–8000 Hz) than the middle-age group. Similar to previous studies (e.g., Ross et al., 2007; Grose and Mamo, 2010), Papesh et al. (2017) showed a decline in IPD change detection with increasing carrier frequency and increasing age, based on N1 and P2 amplitude and latency measures. They also showed that hearing loss imposed further frequency limitations on IPD coding in both the middle age and older hearing-impaired groups. Although cortical measures of IPD processing are not direct measures of binaural encoding of IPD, which is thought to begin in the brainstem (Haywood et al., 2015; Ross et al., 2007), nor are they direct measures of spatial release from masking (SRM), they do rely on effective temporal coding of interaural acoustic change and thus may reflect neural processing necessary to achieve benefits from speech spatial release. As such, Papesh et al. (2017) showed that cortical measures of N1 latency, N1, P2, and N1/P2 amplitude were more strongly predictive of SRM among the four groups studied than were age, hearing loss or age plus hearing loss combined; however, a given neural measure was not necessarily the best predictor for the same group or for the same conditions. Nonetheless, studies that demonstrate correlations between behavior and electrophysiology provide promise for the potential use of electrophysiological measures as objective predictors of speech in noise performance.

6. Summary

The impact of aging on auditory function and auditory perception has been investigated across many different dimensions. Here, we have provided a limited review of recent data from our laboratory as well as others to highlight how age can influence measures of binaural and spatial processing. In particular, both behavioral and electrophysiological measures have shown that aging leads to declines in the ability to process interaural cues such as ITDs, IPDs, and ILDs. In addition, when trying to detect signals in noise, the ability to use interaural cues to aid in the release from masking (e.g., BMLD) also declines with advancing age. Results from a number of investigations suggest that these age-related deficits, often independent of hearing loss, are linked to declines in the auditory system's ability to encode the rapid temporal fine structure in the acoustics of both simple and complex speech and non-speech stimuli. Furthermore, the perception and localization of sounds in more natural environments (i.e., free field) also reveals deficits in older adults, with and without hearing loss, in their ability to take advantage of rich spatial cues when detecting target speech from spatially-segregated competing speech.

Electrophysiological results show that spatial attention to non-

speech stimuli elicits age-related differences in cortical activation to attended spatial targets, where younger adults have larger magnitude responses as well as greater asymmetric activity in one hemisphere versus the other, depending on the hemifield of the sound source. Older adults, on the other hand, typically have smaller magnitude responses, notably in a continuous stimulation paradigm, and reduced hemispheric asymmetry. These results are consistent with the hypothesis that age may lead to both poorer temporal synchrony and broader cortical activation, possibly due to compensatory mechanisms that involve reduced inhibitory drive or dedifferentiation of activation. This result parallels cortical changes observed during studies of cognitive function. Further research is warranted to help delineate the potential age-related neural mechanisms associated with declines in binaural and spatial processing and to identify viable approaches for therapeutic intervention to improve processing and ameliorate such deficits.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.heares.2018.05.001>.

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