Spring 2017

The neural representation of frequency in quiet and noise across the adult life span

Alexandra Bove
James Madison University

The Neural Representation of Frequency in Quiet and Noise Across the Adult Life Span

Alexandra Bove

A dissertation submitted to the Graduate Faculty of

JAMES MADISON UNIVERSITY

In

Partial Fulfillment of the Requirements

for the degree of

Doctor of Audiology (Au.D.)

Department of Communication Sciences and Disorders

May 2017

FACULTY COMMITTEE:

Committee Chair: Christopher Clinard, Ph.D.

Committee Members:

Lincoln Gray, Ph.D.

Brenda Ryals, Ph.D.

Dedication

I would like to dedicate this dissertation to the celiac disease community. Unbeknownst to me, my time in graduate school would begin to unravel years of unanswered questions and lead to the discovery of this diagnosis. I am so grateful for my amazing doctors, Dr. Ciminiello and Dr. Wereley, for believing in me and never giving up. Finishing graduate school would not have been possible without either of you. I'd also like to thank my family, friends, and colleagues for their unwavering support throughout this journey.

Acknowledgements

First and foremost, I would like to thank my dissertation advisor, Dr. Christopher Clinard, for his endless support, guidance, and encouragement. I am so thankful for having had the opportunity to work alongside you throughout this project and for all of the invaluable lessons that you taught me along the way.

I would also like to extend a sincere thank you to my committee members, Dr. Brenda Ryals and Dr. Lincoln Gray, for their invaluable feedback on this project. In addition to serving on my committee, I would especially like to thank Dr. Ryals for her unparalleled mentorship throughout my time at JMU. Your love of audiology and research was infectious; I hope that one day I can inspire students just as you did throughout your career.

Most importantly, I would like to thank my family for all of their support and encouragement along this journey. Mom and Dad, I may have been 415 miles away from home for the past three years, but I felt your support every step of the way. You taught me that I can do anything I set my mind to and have always been the inspiration behind everything that I do. And a special thank you to my big brothers who make me proud each and every day and have always pushed me to do my very best.

Lastly, I am so grateful to have been a recipient of the Roger Ruth Student Memorial Research Grant which was instrumental in providing the funding to make this research project possible. I would also like to thank all of the participants that agreed to devote their time and energy – this project would not have been possible without you all!

Table of Contents

List of Figures

Abstract

The purpose of the present study was to examine why older adults have trouble with speech-in-noise understanding. Difficulty with speech-in-noise comprehension has been associated with age-related degradation in frequency processing. Our study sought to investigate this relationship by examining the neural representation of frequency in quiet and in noise across the adult-life span. In order to do this, one behavioral correlate of frequency processing, frequency difference limens (FDLs), and one electrophysiological correlate, the frequency following response (FFR), was utilized. In the present study, we specifically focus on the electrophysiological measures of frequency processing across the adult life span. It was hypothesized that as age increased, FFR phase coherence and FFR amplitude would decrease (i.e. neural synchrony was expected to degrade with age). It was also hypothesized that masking noise would be expected to have an adverse effect on both FFR phase coherence and amplitude, with older adults having more adverse effects than the younger adults.

Properly identifying the underlying source(s) of impairment is essential to designing appropriate treatment plans that effectively target these underlying deficits. Thus, the present study aims to determine how frequency processing is affected by aging and what consequences it may have on speech-in-noise understanding in older adults.

Chapter I

Review of Literature

Introduction

One of the most common complaints of older adults is that of difficulty

comprehending speech in noise (Dubno, Dirks, & Morgan, 1984; Pichora-Fuller et al.,

1992; Frisina and Frisina, 1997). This is exemplified by older adults who have normal

hearing sensitivity but report considerable difficulty understanding speech in the presence

of background noise. The question still remains as to whether this difficulty is

attributable to degraded peripheral function, age-related changes in the central auditory

system, cognition, motivation, or a combination of these factors. This has led to a surge

of interest in the effects of aging on the auditory system, as properly identifying the

source(s) of the speech-in-noise deficit in aging adults is critical to designing and

implementing appropriate rehabilitation.

Speech-In-Noise Deficits in Older Adults

There has been a great deal of literature that has exemplified and examined these

speech-in-noise deficits in older adults. The overarching question that researchers have

sought to answer is whether or not this deficit in speech-in-noise understanding is

centrally mediated or purely a consequence of peripheral hearing loss. For this reason, a

variety of studies have employed young and older adults, with and without hearing loss,

in order to tease out the effects of hearing loss on speech understanding. These studies

have found that degraded speech-in-noise understanding in older adults is not only a

consequence of degraded peripheral hearing but also due to deficits in the central

auditory system (Dubno et al., 1984; Frisina and Frisina, 1997; Gordon-Salant & Fitzgibbons, 1999).

A study by Dubno, Dirks, and Morgan (1984), showed that the ability to understand speech in background noise was not only determined by hearing acuity but also by the age of the listener. This was exemplified by the fact that age effects were seen in both cohorts of individuals over 65 years of age, those with mild hearing loss and those with normal hearing sensitivity. These age effects, however, were not realized for procedures that did not utilize background noise.

Frisina and Frisina (1997) examined how peripheral and central auditory dysfunctions may play a role in speech-in-noise deficits experienced by elderly adults. One of the main findings from this study was that the speech-in-noise deficits remained in older subjects even when audibility and cognitive functioning were not comprised. These findings suggest that degraded speech processing in older adults may be accounted for by auditory brainstem or auditory cortex temporal-resolution dysfunctions, independent of hearing loss. This is one, of the many studies, that supports the notion that poor speech comprehension does not reside solely in the cochlea, but also within the central auditory system.

Gordon-Salant and Fitzgibbons (1999) sought to further investigate the temporal processing abilities of young and older adults, with and without hearing loss. These researchers examined age-related performance using a variety of speech and non-speech measures in order to assess which measures are most affected by auditory aging. Select speech recognition tasks revealed age-related differences, with older adults having poorer

performance than younger adults on all time compressed speech tasks and tasks containing background noise. This finding suggests that aging imposes a limitation on processing rapid speech segments and this deficit is likely due to deterioration of central timing mechanisms.

Age-related declines in frequency processing are thought to underlie degraded speech-in-noise understanding in older adults. Various studies have proposed that declines in the representation of temporal fine structure (TFS), or the fast oscillations contained within the temporal envelope, may be responsible. The frequency content that is extracted from the TFS of a stimulus is an essential component to understanding speech in everyday listening situations. It not only aids in helping to differentiate speech sounds, such as in formant transitions, but also in improving speech understanding given unfavorable signal-to-noise conditions (Drennan et al., 2007). Prior research has cited several physiological mechanisms as contributing factors to degraded temporal fine structure and frequency processing in older age, one of these being temporal jitter, or a variance in neural synchrony (Pichora-Fuller and Schneider, 1992; Pichora-Fuller et al., 2007).

Pichora-Fuller and Schneider (1992) suggested a model in which binaural processing in older adults is characterized by relatively broader critical bandwidths and higher overall amounts of temporal jitter. In a follow-up study by Pichora-Fuller et al. (2007), researchers temporally jittered the speech signal in order to disrupt the fine structure of the signal and examine how this distortion may affect word identification. Researchers found that speech understanding in noise was significantly degraded in young, normal-hearing adults given sentences that were artificially jittered at frequencies

below 1.2 kHz. It should be noted that, in this region, phase locking is likely to be involved. In addition, the accuracy with which the young subjects identified the jittered speech was similar to that of older adults with good audiograms when listening to unaltered speech-in-noise. Lastly, this study revealed that spectral distortion could not account for this finding and that temporal distortion was the mechanism that was likely responsible for degraded word identification in noise. Ultimately, these studies were integral in suggesting that temporal jitter has adverse effects on speech understanding in noise and that these deficits arise in the aging auditory system.

Age-related Changes in Frequency Processing: Behavioral Studies

Various studies have sought to investigate frequency processing in humans using behavioral tasks in order to assess which neural code (e.g. temporal, rate-place) is being used and have added to the growing body of literature demonstrating age-related deficits in frequency processing. Multiple studies have shown that age-related declines on behavioral frequency discrimination limens and frequency modulation detection limens are greatest at low frequencies (e.g., 500 Hz), consistent with poorer phase locking being a contributing factor [Moore et al., 1992; He et al., 1998; He et al., 2007; Clinard et al., 2010]. Furthermore, these age-related deficits in frequency processing can occur as early as middle-age (He et al., 2007; Clinard et al., 2010).

He, Dubno, and Mills (1998) investigated frequency discrimination in younger and older adults with closely matched audiograms. These researchers found that frequency discrimination was degraded and more variable in older individuals versus young individuals. The largest effects were observed at 500 Hz, and smaller effects were seen with increasing frequency. Given that this age-related deficit was significantly

greater at the low frequencies, this reduction in frequency discrimination is consistent with age-related declines in phase locking.

A subsequent study by He, Dubno, & Mills (2007) investigated the effects of aging on frequency modulation detection. Subjects included younger and older individuals with normal hearing (e.g. <20 dB HL from 250 to 4 kHz). In this study, researchers found a frequency-dependent effect on frequency modulation (FM) detection with aging having the largest effect. FM detection was significantly poorer for older subjects, with larger differences noted at low carrier frequencies (e.g. 500 Hz) than at high carrier frequencies (e.g. 4 kHz). The findings from the FM detection task align with prior studies on frequency discrimination, thus the authors suggest that there may be a shared underlying mechanism at play, related to temporal processing. The authors suggest that one such mechanism may be explained by phase locking which is robust at low frequencies and then declines with increasing frequency. It is plausible that this mechanism may degrade with age, consistent with findings from He et al. (1998).

Altogether, these studies revealed age-related deficits that are more prominent at lower frequencies in comparison to higher frequencies. One plausible explanation for this finding is a decline in phase locking ability that occurs in the aging auditory system. According to Palmer et al. (1986), the frequency coding of low frequency stimuli is largely represented by phase-locking in animal models. It should be noted that the upper limit of phase locking is species-specific. However, in general, the ability of auditory nerve fibers to phase lock decreases with stimulus frequency (Palmer et al., 1986). Given that prior behavioral studies have consistently demonstrated age-related

deficits at low frequencies, it is plausible that a subsequent decrease in phase-locking ability may take place in the aging auditory system and account for this finding.

Frequency Representation in Quiet and in Noise

Temporal coding and rate-place coding are both involved in the encoding of frequency. Temporal coding (i.e. phase locking) is involved in the frequency coding of low-to-mid frequency information. In select animal models, phase locking is robust at and below 1 kHz, after which it begins to decline (Palmer & Russell, 1986). Beyond this point, multiple neurons are needed to encode frequency (e.g. volley theory). Rate-place coding is considered to be the mechanism largely responsible for frequency coding beyond the upper limit of phase locking. Single-unit animal studies have demonstrated that low, medium, and high spontaneous firing rate fibers can represent frequency in quiet using rate-place coding (e.g., Shofner & Sachs, 1986). However, only low spontaneous rate, high threshold fibers are able to adequately represent frequency in noise (Costalupes, 1985; Young and Barta, 1986).

In everyday listening situations, we use a blend of these mechanisms to encode frequency information. We need to keep in mind that everyday listening environments typically have some degree of background noise and therefore, must consider the effects of noise on frequency coding.

Shofner and Sachs (1986) revealed that while low, medium, and high spontaneous rate fibers are all able to adequately represent frequency at low intensity levels (34 dB SPL), only select populations of fibers can adequately represent frequency given high intensity levels. Specifically, the researchers found that the low spontaneous

rate, high threshold fibers are critical for encoding frequency information at high sound pressure levels (87 dB SPL). In contrast, the high and medium spontaneous rate fiber population saturates given the high intensity stimulus level and cannot adequately represent frequency.

Other animal physiology studies have incorporated background noise and have revealed that rate-place coding deteriorates in the presence of noise while temporal coding remains largely unaffected. In a study by Costalupes (1985), high-spontaneous rate fibers became saturated by high-intensity noise and were unable to adequately represent frequency in noise at SNRs close to and slightly above behavioral detection thresholds. In contrast, rate-place representation endured among low and medium spontaneous rate fibers in moderate to high levels of noise (26 - 46 dB SPL tone intensity with 29 dB SNR). This study is consistent with others that show that low spontaneous rate fibers are primarily responsible for the encoding of frequency information in noise (Young & Barta, 1986). The higher thresholds and wider dynamic ranges characteristic of low and medium SR fibers are thought to make them more resistant to saturation by high level noise. Furthermore, Schmeidt et al. (1996) showed that there is a loss of these low-spontaneous rate fibers in aging gerbils, which also may account for (or contribute to) some of the speech-in-noise deficits experienced by older adults.

Frequency-Following Response

The frequency-following response is an auditory evoked potential that is dependent on phase-locked neural activity (Worden & Marsh, 1968). This response allows us to quantify the degree of phase locking in humans (Dobie et al., 1989). When recorded from the scalp, the primary neural generator is thought to be the Inferior

Colliculus (Smith et al., 1975). In humans, the FFR has an upper limit between roughly

1.5 kHz and 2 kHz due to the upper limit of phase locking [in scalp recordings]

(Krishnan, 2007). Because the FFR allows us to measure phase-locked neural activity,

we are able to assess neural synchrony across the aging auditory system.

Clinard et al. (2010) examined phase-locked neural activity in response to tones in

quiet utilizing the FFR. It was found that the neural representation of frequency was

degraded in middle-aged and older adults, as depicted by poorer FFR phase coherence

and amplitude. These declines were frequency-dependent; with significant age effects

seen in response to 1000 Hz tones but not 500 Hz tones, in quiet. These findings are

consistent with the temporal jitter hypothesis, as we would expect to see greater variance

in neural synchrony (and thus reduced phase locking) at higher stimulus frequencies. In

other words, we would expect that temporal jitter would have more adverse effects on the

encoding of higher frequency stimuli than lower frequency stimuli.

Conclusion

Despite the fact that hearing in noise is one of the most common complaints of

aging individuals, the neural representation of frequency in noise, using the FFR, has not

been extensively studied. In the present study, we hope to expand on the literature by

examining the effects of age on the neural representation of frequency in quiet and in

noise. The objective of the proposed research is to specifically examine how background

noise affects phase-locked neural representations of frequency across the adult life span.

The present study employed masking noise in order to cause maximal disruption of rate-

place frequency coding and attempt to force listeners to rely on temporal coding for

sounds in the region of robust phase-locking (i.e. 500 and 1000 Hz) in a separate

dissertation that focuses on behavioral measures of frequency discrimination in noise. By doing so, we hypothesized that significant age-effects will be seen, as older individuals will largely have to rely on an impaired temporal coding mechanism.

In order to quantify the neural representation of frequency in quiet and in noise, the present research utilized the electrophysiological measure, the FFR, to measure the phase locked response of auditory brainstem neurons. Ultimately, we are able to address the temporal-jitter hypothesis in humans by quantifying phase locking across the adult life span.

In the present study, the following hypotheses were addressed:

1) It was hypothesized that FFR phase coherence and FFR amplitude would worsen with age (i.e. neural synchrony is expected to degrade with age). It was also hypothesized that there would be an age X frequency interaction, with significant age-related FFR declines expected at 1000 Hz.

2) It was expected that masking noise would have an adverse effect on both FFR phase coherence and amplitude, with the masking noise having more adverse effects on older adults in comparison to younger adults.

Chapter II

Materials and Methods

    Subjects

Fourteen subjects (1 male, 13 females) between the ages of 21 and 66 participated in this experiment. These participants were divided into three groups: young (n = 5, age range 21 to 22, mean age = 21.8, 5 females); middle-aged, ages 43 to 53 (n = 4, mean age = 47.5, 4 females); and older, ages 61 to 66 (n = 5, mean age = 62.4, 1 male, 4 females). All subjects in the study were required to have normal hearing acuity, defined as thresholds better than or equal to 25 dB HL at octave frequencies from 250 to 4000 Hz. All subjects were monolingual, native English speakers. Exclusion criteria included abnormal tympanometric measures or any history of otologic or neurologic pathology. A GSI-39 tympanometer was used as the primary screening tool. Subjects primarily included students, staff, and faculty from James Madison University. Participants were recruited through fliers, emails, and word of mouth. All subjects were compensated for voluntary participation in the study. The institutional review board (IRB) at James Madison University approved all of the procedures outlined in this study. Subjects were tested using both electrophysiological and perceptual measures, including tone-in-noise detection, frequency discrimination limens, and frequency-following response (FFR) testing at 500 and 1000 Hz.

    Stimuli

The stimuli for the behavioral and physiological conditions were tonebursts of 250 ms duration, including a 15-ms rise/fall time shaped by a Hanning window. 70 dB

SPL tonebursts were delivered to the right ear through magnetically-shielded ER3-A insert earphones for the physiological conditions. Tones-in-noise were delivered using octave-wide noise centered on a test frequency (500 Hz or 1000 Hz). Tones were created using a sampling rate of 44.1 kHz. Magnetically shielded insert earphones with extended earphone tubing were used to minimize the potential of recording electromagnetic artifact.
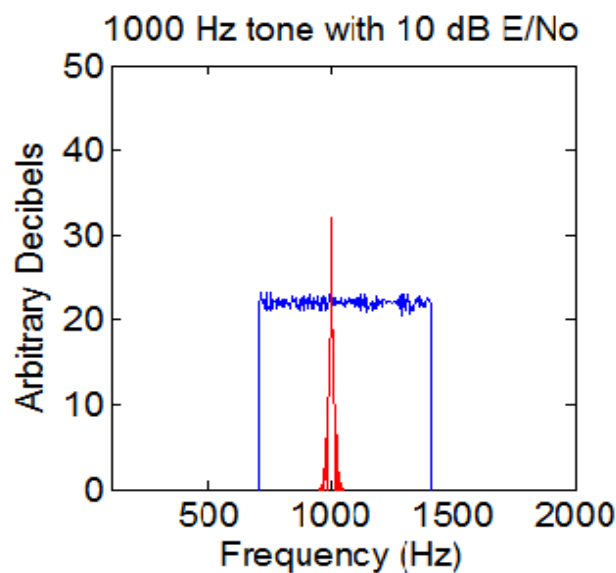
Figure 1. Example stimulus spectrum of a 1000 Hz tone with octave-wide noise centered around the stimulus frequency.

FFR Recordings

The frequency-following response was recorded at 500 Hz and 1000 Hz in three separate conditions: Quiet, +5 dB, and +10 dB. The latter two conditions were relative to the individual's 91% correct point on a tone-in-noise detection task at the same frequency (e.g. 500 or 100 Hz); the tone-in-noise detection task was performed as part of a separate dissertation focusing on behavioral measures of frequency in noise. The acoustic SNR in

the +5 condition would be 5 dB greater than the SNR corresponding to an individual's 91% correct point for a given frequency. This approach is common in frequency-discrimination-in-noise literature (e.g., Dye and Hafter, 1980). The order of the six conditions was randomized for every participant and a five-minute break was allotted between each FFR condition. FFRs were collected using a one-channel electrode montage with a Neuroscan SynampsRT acquisition system. FFRs were recorded from Cz (active) to the nape-of-neck (reference), with the ground electrode located on the forehead. The inter-stimulus interval (ISI) was set to 516.67 secs. An analog to digital sampling rate of 20 kHz was used. Tones were presented using 100 randomly ordered versions of narrowband noise so as to prevent phase locking to the temporal envelope of the noise. One thousand artifact-free sweeps were collected per condition. Online artifact rejection was performed, excluding sweeps that exceeded the rejection criterion of $\pm$ 30 μV. In select cases, the online artifact rejection criterion had to be raised due to EKG artifact exceeding $\pm$ 30 μV. All electrode impedances were below 5 kΩ and inter-electrode impedances fell within 1 kΩ. Impedance was recorded prior to every condition. Online electroencephalography (EEG) filters were 30-3000 Hz and the acquisition time window was from 0-260 ms. All subjects were seated in a reclining chair during testing and were given instructions to relax quietly for the duration of the recording. All recordings were performed in a double-walled, sound-attenuated booth. Data collection typically involved one session with a total duration of two to four hours.

FFR Analysis

In order to quantify neural synchrony, the frequency-following response was analyzed off-line using two metrics: phase coherence and amplitude. Both analyses were

performed on the output of a Fast Fourier Transform (FFT). A custom Matlab program was used in order to determine response presence or absence.

The first metric, phase coherence, reveals the degree of phase locking to the stimulus frequency. Phase data across consecutive pairs of sweeps were extracted from the stimulus frequency's FFT bin. The Rayleigh test (Fisher, 1993), which assesses circular uniformity, was used in order to evaluate the degree of phase locking and determine response presence ($p<0.05$) or absence ($p>0.05$). The scale extends from 0 to 1 or from random phase to perfect phase locking, respectively. It should be noted that the phase coherence metric looks at the consistency of phase locking, not where on the wave that it locks onto. All phase coherence measures were calculated using non-averaged concatenated sweeps, as this allows the measure to be independent of response amplitude.

The second metric, response amplitude, depicts the averaged neural response magnitude.   In order to calculate the response amplitude, averaged concatenated sweeps were submitted to a FFT in order to determine response presence or absence. The response amplitude was measured from the FFT bin of the stimulus frequency. If present, the FFR amplitude was greater than 6 dB above the background noise (i.e. 6 dB SNR). The background noise was estimated using the mean of five FFT bins above and below the stimulus frequency (i.e. $\pm$ 10 Hz). Thus, the response was determined to be present ($p<0.05$) if the amplitude was significantly greater than the surrounding noise and absent ($p>0.05$) if the amplitude was not significantly greater than the surrounding noise.
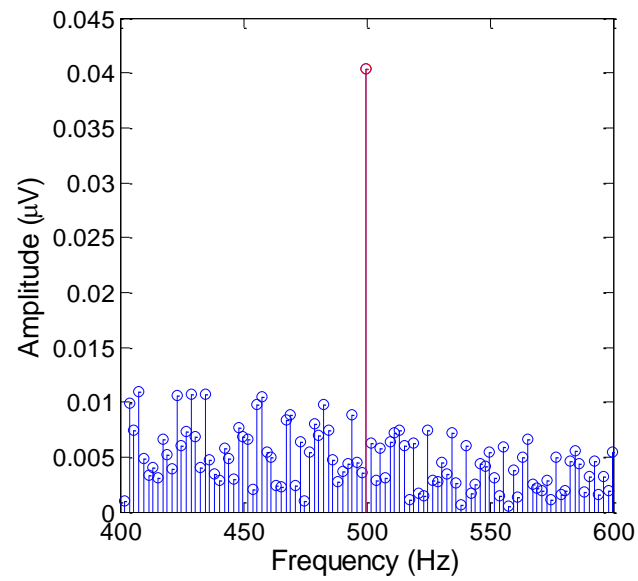
Figure 2. Individual FFR Data from a young subject (age 22). This FFT output from a 500 Hz FFR waveform reveals a present response at the stimulus frequency, 500 Hz. The red line represents the amplitude of the response and the blue lines represent the surrounding noise.

Chapter III

Results

Two repeated-measures analyses of variance (ANOVA) were performed with either FFR phase coherence or amplitude as the dependent variable. Factors were group (between subjects, three levels: young, middle-aged, or older group), frequency (within subjects, two levels: 500 Hz or 1000 Hz), and noise (within subjects, three levels: quiet, +5, and +10).

Frequency Following Response: Amplitude

A 3 x 2 x 3 repeated-measures ANOVA with factors of group (between subjects), frequency (within subjects), and noise (within subjects) was performed. The main effects of frequency [$F_{(1,11)} = 6.062$, $p = 0.032$, partial $\eta^2 = 0.355$] and group [$F_{(2,11)} = 5.135$, $p = 0.027$, partial $\eta^2 = 0.483$] were significant, with notable effect sizes. Main effect of noise [$F_{(2,22)} = 1.432$, $p = 0.261$] was not significant (see Figure 3). No interactions were significant (p>0.05). Pairwise comparisons by group revealed that the younger and older groups were significantly different (p=0.008). The findings suggest that there was a frequency dependent effect on amplitude. The FFR amplitude was significantly larger for the 500 Hz conditions in comparison to the 1000 Hz conditions. This trend was anticipated due to expected patterns in FFR amplitude across frequency (e.g. Clinard et al., 2010). There was also a significant effect of group (e.g. young, middle, or older) on FFR amplitude. As age increased, FFR amplitude decreased. Of interest, there was no significant effect of noise on FFR amplitude, thus the octave-wide noise did not appear to adversely affect FFR amplitude.
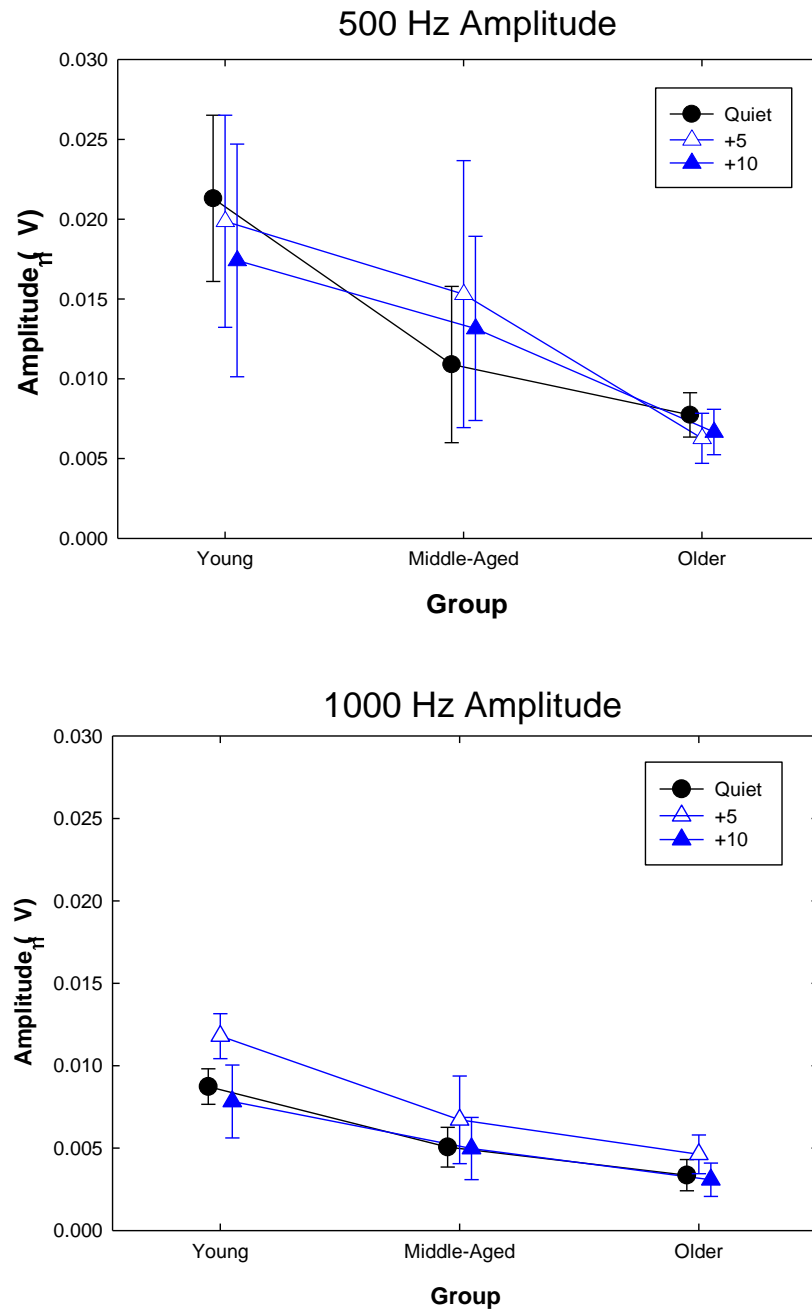
Figure 3. FFR amplitude is shown for 500 Hz (top graph) and 1000 Hz (bottom graph) across group and the three noise conditions: Quiet, +5, +10 dB. Circles represent the quiet condition, open triangles represent the +5 dB condition, and filled triangles represent the +10 dB condition. Error bars represent the standard error of the mean. Data points have been slightly offset along the abscissa in order to minimize overlapping data points.

Frequency-Following Response: Phase Coherence

A 3 x 2 x 3 repeated-measures ANOVA with factors of age, frequency, and noise was performed. The main effect of group [$F_{(2,11)} = 9.986$, $p = 0.003$, partial $\eta^2 = 0.645$] was significant. Pairwise comparisons by group revealed that the middle-aged and older groups were significantly different than the younger-aged group ($p<0.018$). Main effects for frequency [$F_{(1,11)} = 002$, $p = 0.965$] and noise [$F_{(2,22)} = 2.214$, $p = 0.158$] were not significant (see Figure 4). No interactions were significant. The findings suggest that there was an effect of age on phase coherence. Phase coherence was less robust in aging adults in comparison to younger adults. Post-hoc analysis revealed that younger adults had significantly better phase coherence measures in comparison to both middle-aged and older adults. FFR phase coherence, however, was not significantly affected by the frequency of the stimulus or the noise conditions.

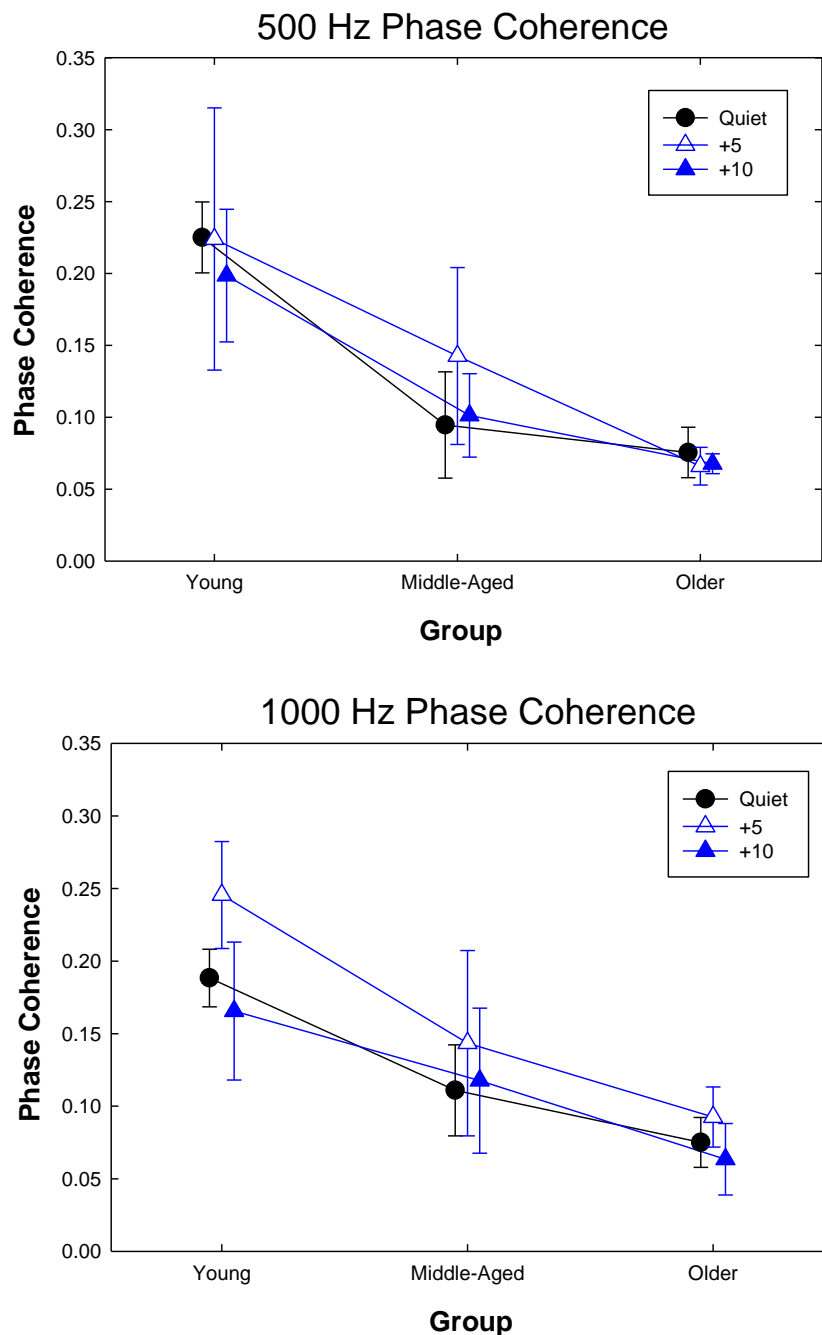**Figure 4.** FFR phase coherence is depicted for the 500 Hz (top) and 1000 Hz (bottom) stimuli across group and the three noise conditions: Quiet, +5, +10 dB. Circles represent the quiet condition, open triangles represent the +5 dB condition, and filled triangles represent the +10 dB condition. FFR phase coherence became poorer as age increased. Error bars represent the standard error of the mean.

Chapter IV

Discussion

The current study examined the effects of aging on the neural representation of frequency in quiet and in noise. Masking noise was utilized in order to cause maximal disruption of rate-place coding and attempt to force subjects to rely on temporal coding for tones in the region of robust phase-locking (e.g. 500 and 1000 Hz), for behavioral measures tested in a separate dissertation. The present study utilized the frequency-following response in order to quantify the degree of phase-locking in young, middle-aged, and older subjects. It was hypothesized that FFR phase coherence and FFR amplitude would decline with age. An age by frequency interaction was expected, with larger age-related declines expected at 1000 Hz versus 500 Hz. It was also hypothesized that masking noise would adversely affect both FFR phase coherence and amplitude, having more detrimental effects on older adults in comparison to younger adults.

The present study revealed an aging effect, with reduced phase coherence for older adults in comparison to younger adults. Across subjects, FFR amplitudes were more robust at lower frequencies in comparison to higher frequencies, consistent with previous findings (Clinard et al., 2010). FFR amplitudes were significantly less robust for older individuals in comparison to younger individuals, suggesting a significant effect of age on amplitude. The findings for an age-dependent decline in phase coherence and amplitude is consistent with prior literature.

Clinard et al. (2010) found that, in older adults, phase-locking for frequencies near 1000 Hz was significantly less robust than for frequencies near 500 Hz. This trend

was demonstrated in the present study. As Clinard et al. (2010) suggested, temporal jitter may be a possible explanation for this trend. It is possible that temporal jitter has a larger effect on the 1000 Hz stimuli due to its shorter period, which may result in a reduced upper phase locking limit in older subjects. Thus, this age-dependent decline in amplitude and phase coherence is consistent with Clinard et al. (2010), and provides evidence for an age-related decline in phase locking ability.

It should be noted, however, that declines in neural synchrony can also occur due to various other factors, including changes in the periphery and/or central auditory system. For example, decreased neural inhibition and longer neural recovery time are two physiologic mechanisms that may contribute to age-related declines in frequency processing. Thus, although our study is consistent with prior literature proposing an age-related decline in phase locking, other extraneous variables must also be considered.

There is a lack of research showing age-related changes in phase-locked neural activity, hindering our ability to compare our data to other studies. The present study is one of the few studies that have investigated phase-locked neural activity in quiet and noise across the adult life-span using a simple pure tone stimulus. Thus, results from this study are novel and contribute to the body of literature investigating phase-locked neural activity in humans.

Clinical Relevance

Speech-in-noise deficits in older adults are well documented in the literature and exemplify the difficulty that many older adults face in everyday listening situations. Cruickshanks et al. (1998) investigated the prevalence of hearing loss and found that for

every five years of age, the risk of hearing loss increases by nearly 90%. As we know, peripheral hearing loss degrades speech-in-noise understanding by reducing the fidelity of the stimulus. Unraveling other deficits (i.e. temporal processing) that contribute to this difficulty in speech-in-noise is critical to designing appropriate rehabilitation that can better target these deficits.

While this study did not directly investigate speech-in-noise deficits in older adults, it adds to the body of literature proposing degradation in phase-locking ability as one of the contributing factors. Further studies that investigate how age-related declines in the periphery and/or central auditory system contribute to poor speech-in-noise understanding are integral. Properly identifying the source(s) of impairment is critical to designing appropriate rehabilitation for older adults and will provide further insight on the difficulty that many aging adults face when it comes to speech-in-noise comprehension.

Auditory Training

Because a two-fold problem often presents with older individuals, that being peripheral and central deficits, amplification has its limitations. Because of this, supplementary treatment strategies must be considered that can better target these underlying central deficits and help to improve speech-in-noise perception. Recent literature on the use of auditory training shows promise for rehabilitation. Recent studies have demonstrated neural plasticity in the auditory system of both animals (Gao & Suga, 2000) and humans (Tremblay et al., 2001; Tremblay & Kraus, 2002).

Recent studies have illustrated the effects of training on frequency coding, specifically using the frequency-following response. For example, Song et al. (2008) trained native English-speakers to utilize foreign speech stimuli (i.e. lexical pitch patterns) in word identification tasks. Researchers then measured pitch tracking via the FFR, before and after training. The results showed significant effects of training as the participants had increased pitch-tracking accuracy and demonstrated that auditory training can have neural implications. A more recent study by Carcagno & Plack (2010) also showed significant effects of pitch discrimination training on the FFR in a group of adult subjects with the trained subjects showing significant improvements in pitch discrimination in comparison to controls. Of interest, FFR phase locking to the envelope significantly increased in trained subjects. This study was integral in showing that even low-level processes within the human auditory system can be influenced by auditory training. Thus, all of these studies were key in showing the plasticity of the auditory system and that training may be used to remediate underlying deficits.

It should be noted that the majority of the studies cited above investigated the temporal envelope. Our study utilized a tone-evoked FFR, thus, it is unknown as to what changes auditory training may have using this type of stimulus and even further, what consequences this may have on speech-in-noise perception. However, our study holds promise in that the FFR may be useful in identifying those individuals with degraded temporal processing that may benefit from auditory training. Future studies with the FFR should encompass a behavioral correlate, such as speech-in-noise perception, or a binaural processing task, that better reflects the difficulties that older adults face in everyday listening environments.

Future Directions

Future research may encompass individuals with age-related hearing loss or utilize more complex stimuli that better represent naturally produced speech. As mentioned, there has been a paucity of research specifically investigating the effects of aging on phase-locked neural activity. For this reason, our study employed a simple, pure-tone stimulus in order tease out the effects of language, cognition, etc. that are factors when utilizing speech stimuli. Future studies may choose to utilize more complex stimuli, such as naturally-produced speech, in order to investigate if similar effects would be seen with a more realistic stimulus. Given that older adults complain of difficulty comprehending speech-in-noise, a future study utilizing speech stimuli in the presence of background noise may be better able to generalize to the difficulties that many older adults face on a daily basis.

Future studies may also encompass individuals with age-related hearing loss. Our study consisted of individuals with normal hearing from 250 Hz to 4 kHz, and as will be discussed later, may encompass a unique subset of middle-aged or older individuals. Instead of utilizing individuals with normal hearing across the adult life-span, future studies may encompass individuals with age-related hearing loss and younger individuals with matched audiograms. While the effects of hearing loss cannot be teased out in this type of study design, it has the benefit of more accurately reflecting the population of older individuals with some degree of age-related hearing loss. Given the effects of hearing loss plus degraded frequency processing in older individuals, it is plausible that larger effects may be seen.

Methodological Issues

As mentioned, our study solely encompassed young, middle-aged, and older individuals with normal hearing (e.g. 250 Hz to 4 kHz). Because of this, our group of older individuals may comprise a unique subset of older individuals that may not accurately represent the majority of older individuals with speech-in-noise deficits. Furthermore, our study employed noise at +5 and +10 dB signal-to-noise ratios (i.e. 5 or 10 dB above the individual's tone-in-noise discrimination on a behavioral task). It is possible that if we had encompassed a broader range of SNRs, larger effects may have been seen.

Conclusions

1. FFR amplitudes for the 500 Hz conditions were significantly larger than those for the 1000 Hz conditions, as expected. There was a significant effect of age on FFR amplitude, with FFR amplitude decreasing as age increased.

2. FFR phase coherence became significantly poorer as age increased, consistent with an age-related decline in frequency representation. Younger subjects had significantly better (i.e. more robust) phase coherence measures in comparison to both middle-aged and older subjects.

3. FFR amplitude and phase coherence measures were not significantly affected by the noise conditions for any age group.

References

Carcagno, S., & Plack, C. J. (2011). Subcortical plasticity following perceptual learning in a pitch discrimination task. *Journal of the Association for Research in Otolaryngology*, *12*(1), 89-100.

Clinard, C.G., Tremblay, K., Krishnan, A. 2010. Aging alters the perception and physiological representation of frequency: Evidence from human FFR recordings. *Hearing Research 264*, 48-55.

Costalupes, J.A. 1985. Representation of tones in noise in the responses of auditory nerve fibers in cats. I. Comparison with detection thresholds. *The Journal of Neuroscience 5*, 3261-9.

Cruickshanks, K. J., Wiley, T. L., Tweed, T. S., Klein, B. E., Klein, R., Mares-Perlman, J. A., & Nondahl, D. M. (1998). Prevalence of hearing loss in older adults in Beaver Dam, Wisconsin the epidemiology of hearing loss study. *American Journal of Epidemiology*, *148*(9), 879-886.

Dobie, R. A., & Wilson, M. J. (1989). Analysis of auditory evoked potentials by magnitude-squared coherence. *Ear and hearing*, *10*(1), 2-13.

Drennan, W. R., Won, J. H., Dasika, V. K., & Rubinstein, J. T. (2007). Effects of temporal fine structure on the lateralization of speech and on speech understanding in noise. *Journal of the Association for Research in Otolaryngology*, *8*(3), 373-383.

Dubno, J. R., Dirks, D. D., & Morgan, D. E. (1984). Effects of age and mild hearing loss on speech recognition in noise. *The Journal of the Acoustical Society of America*, *76*(1), 87-96.

Dye Jr, R. H., & Hafter, E. R. (1980). Just-noticeable differences of frequency for masked tones. *The Journal of the Acoustical Society of America*, *67*(5), 1746-1753.

Fisher, N. I. (1993). *Statistical analysis of circular data*. Cambridge University Press.

Frisina, D. R., & Frisina, R. D. (1997). Speech recognition in noise and presbycusis: relations to possible neural mechanisms. *Hearing research*, *106*(1-2), 95-104.

Gao, E., & Suga, N. (2000). Experience-dependent plasticity in the auditory cortex and the inferior colliculus of bats: role of the corticofugal system. *Proceedings of the National Academy of Sciences*, *97*(14), 8081-8086.

Gordon-Salant, S., & Fitzgibbons, P. J. (1999). Profile of auditory temporal processing in older listeners. *Journal of Speech, Language, and Hearing Research*, *42*(2), 300-311.

He, N., Dubno, J. R., & Mills, J. H. (1998). Frequency and intensity discrimination measured in a maximum-likelihood procedure from young and aged normal-hearing subjects. *The Journal Of The Acoustical Society Of America, 103*(1), 553-565.

He, N. J., Mills, J. H., & Dubno, J. R. (2007). Frequency modulation detection: effects of age, psychophysical method, and modulation waveform. *The Journal of the Acoustical Society of America*, *122*(1), 467-477.

Krishnan, A. (2007). Frequency-following response. In R. F. Burkard, M. Don, & Eggermont (Eds.), *Auditory evoked potentials: Basic principles and clinical application* (pp. 313-329). Philadelphia, PA: Lippincott Williams & Wilkins.

Moore, B. C., & Peters, R. W. (1992). Pitch discrimination and phase sensitivity in young and elderly subjects and its relationship to frequency selectivity. *The Journal Of The Acoustical Society Of America, 91*(5), 2881-2893.

Palmer, A. R., & Russell, I. J. (1986). Phase-locking in the cochlear nerve of the guinea-pig and its relation to the receptor potential of inner hair-cells. *Hearing Research, 24*(1), 1-15.

Pichora-Fuller, M.K., Schneider, B.A. 1992. The effect of interaural delay of the masker on masking-level difference in young and old adults. *Journal of the Acoustical Society of America 91*, 2129-2135.

Pichora-Fuller, M. K., Schneider, B. A., Macdonald, E., Pass, H. E., & Brown, S. (2007). Temporal jitter disrupts speech intelligibility: a simulation of auditory aging. *Hearing Research, 223*(1-2), 114-121.

Schmiedt, R. A., Mills, J. H., & Boettcher, F. A. (1996). Age-related loss of activity of auditory-nerve fibers. *Journal of neurophysiology*, *76*(4), 2799-2803.

Shofner, W. P., & Sachs, M. B. (1986). Representation of a low-frequency tone in the discharge rate of populations of auditory nerve fibers. *Hearing research*, *21*(1), 91-95.

Song, J. H., Skoe, E., Wong, P. C., & Kraus, N. (2008). Plasticity in the adult human auditory brainstem following short-term linguistic training. *Journal of Cognitive Neuroscience*, *20*(10), 1892-1902.

Tremblay, K. L., & Kraus, N. (2002). Auditory training induces asymmetrical changes in cortical neural activity. *Journal of Speech, Language, and Hearing Research*, *45*(3), 564-572.

Tremblay, K., Kraus, N., McGee, T., Ponton, C., & Otis, B. (2001). Central auditory plasticity: changes in the N1-P2 complex after speech-sound training. *Ear and hearing*, *22*(2), 79-90.

Worden, F. G., & Marsh, J. T. (1968). Frequency-following (microphonic-like) neural responses evoked by sound. *Electroencephalography and Clinical Neurophysiology, 25*(1), 42-52.

Young, E. D., & Barta, E. B. (1986). Rate responses of auditory nerve fibers to tones in noise near masked threshold. *J. Acoustic. Soc. Am., 79(2),* 426-442.