The Neural Correlates of Broad Bandwidth and Narrow Bandwidth Elevated Sound

by

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A Thesis Submitted in Partial Fulfillment
of the Requirements for the Degree of
Master of Arts in Quantitative Psychology

Middle Tennessee State University
2013

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ACKNOWLEDGEMENTS

Many people have played an integral role throughout the creation of this thesis. I acknowledge Dr. Alan Musicant for the guidance he has provided. With the unwavering support he has shown, and in his ability to remain curious, and seek answers, he has demonstrated the best in humanity. I thank Dr. Cyrlle Magne for his insight and collaboration on the thesis. He has given many hours to the project and I am grateful to have been able to work with him. I express gratitude to Dr. Dana Fuller for the support, knowledge, and insight she has provided over the years. I would not have developed an enthusiasm for statistics without the excitement and passion she has shown.

I acknowledge Dr. Will Langston for his contribution in the early stages of the project. I am grateful to Dr. Sohee Park for instilling in me a passion for experimentation and research. Finally, I express a deep sense of gratitude to J. Aaron Albritton. This thesis is a result of his friendship and the sacrifices he has made to assure my wellbeing.

ABSTRACT

The present study aimed to investigate the N1 response for both narrow band and

broadband sound in order to better understand auditory spatial localization, as well as the

role of the "where" stream for localizing elevated sound. Electroencephalographic

recordings were obtained from subjects as they listened to broadband or narrowband

sounds, with center frequencies of either 4 kHz or 10 kHz, presented from five vertical

loud speakers, ±40°, ±20° and 0°. The data did not reveal any clusters that identified

differences in neuronal processing across time for sound type. The auditory evoked

responses demonstrated that, under monaural conditions, narrow band and broadband

sounds are differentially processed in A1. Overall, we could not confirm the use of

different or similar brain resources for horizontal and vertical sound localization, nor

could we demonstrate involvement of the dorsal stream regarding elevated sound

localization.

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CHAPTER I

Introduction

The ability to localize sound, in humans, is crucial for navigation and interaction with

the environment. The hearing range in adults is from 16 Hertz (Hz) to 20,000 Hz

(Rosenberg, pp 10; 1982). Sound location is determined using binaural cues, monaural

cues and the sound's frequency composition (Musicant & Butler, 1984). For instance,

cues important for localizing sounds along the horizontal plane are the interaural time

differences (ITD), the time it takes a sound to reach one ear once a sound has already

reached the opposing ear, and the interaural level differences (ILD), which is a decrease

in sound intensity caused by the head, which leads to a "so-called" head shadow effect.

The pinna of the ear is used for vertical sound localization, acting to modify/filter the

original sound source spectrum to determine direction specific information. These cues,

the ITD, the ILD, and the pinna cues are processed at the neural level, in the midbrain,

the superior olivary complex, the inferior colliculus, and eventually the auditory cortex,

both secondary and primary (A1). A1 is located in the temporal lobe and is within the

core portion of the auditory areas in the brain. Additional areas include the belt and

parabelt area that surround A1. Previous research has shown the importance of A1 for

sound localization, specifically when ILD and ITD are the primary cues utilized (Imig, Irons & Samson, 1990). Further research has shown the importance of areas surrounding A1 in relation to frequency analysis (Rauscheker & Scott, 2009). There is evidence to support at least two auditory streams of information that process distinct properties of the auditory stimulus. One stream processes spatial information (the "where" pathway) while another stream processes object information (the "what" pathway) (Ahveninen et al., 2004; Maeder et al., 2001; Rauschecker & Tian, 2000). The goal of this study is to demonstrate the recruitment of neurons in A1 during vertical sound localization based on the frequency composition of a sound stimulus. Further, we wish to examine the contribution of the auditory 'where' pathway in the cortex and indicate the role of this processing stream, if any role exists, in processing distinct frequency information derived from pinna filtering properties tied to spatial localization.

Localization Cues

Binaural cues. Cues needed for horizontal (azimuth) sound localization are called the interaural time difference and the interaural level difference. The ITD is used for low-frequency sound stimuli, or sounds less than 1500 Hz and takes advantage of the amount of time it takes, for a sound stimulus to travel from one ear to the far ear. The ITD as a

function of azimuth provides a measure of the angular discrepancy of sound. A larger

ITD indicates sound that originated further to the side. For example, the smaller the ITD

the less the angular discrepancy, indicating that the sound source is either more in front of

or more behind where the sound was generated. The larger the ITD, the larger the angular

discrepancy, indicating that the sound source is more left or more right (more to the side)

of the listener. When a sound has an angular measure of 90 degrees, the ITD, for an adult

human, is roughly 650 μs. This is about the largest time difference that occurs in humans.

For high-frequency sounds (sounds 3000Hz or higher) the ILD is used for

azimuthal determinations. The ILD takes advantage of the sound pressure level (SPL)

difference between the two ears caused by an acoustic shadow, which is an area where

there is a reduction in intensity by some object. The head acts as a barrier to reduce the

sound level for frequencies with wavelengths that are smaller than the head. Likewise,

the unobstructed area receiving the higher intensity is the ear closest to the sound source.

Spectral cues. Spectral cues are monaural (one ear) localization cues defined as

the differences in spectral information, as a function of location, of frequencies due to the

modification of sounds by pinnae (outer ear). These cues are needed for localization of

elevated sound (Recanzone & Sutter, 2008). However, spectral cues have an additional

role. Along with binaural cues, the spectral cues are used to localize difficult to discern information, such as sounds originating from the front or back of a listener. According to Recanzone and Sutter (2008), monaural cues can provide information concerning the location of a sound stimulus for both azimuth and the vertical plane.

Spectral Cues and Localization. ITD and ILD are binaural cues used to determine direction of sounds along the horizontal plane (HP). ILD and the ITD are unable to resolve front-rear discriminations. Despite this inability, listeners are able to discern a sound's location within the cone of confusion. Therefore, cues other than the ILD and the ITD must be contributing to a listener's ability to resolve front-back sound localization. Musicant and Butler (1984) demonstrated the use of spectral cues in resolving the localization of sounds originating in the front or rear along the horizontal plane (HP). The authors occluded the pinnae, thus removing the use of spectral cues, and presented sounds to listeners along the HP. When broadband (100 Hz – 16000 Hz) and band limited (1.0 kHz – 4.0 kHz) sounds were presented in front of subjects they mistakenly identified the sounds' location by reporting that the sound had come from the rear. These reversals were noted when sounds were presented from both the rear and the front of the subject. According to Recanzone and Sutter (2008), spectral cues are most

effective when sounds contain broad spectral bandwidth. While the ILD, the ITD, and the

monaural spectral cues of the pinna are critical for determining a sound's location,

additional information is needed in order to locate a sound's exact point of origin.

Frequency Composition. Further information needed to locate a sound's point of

origin are not only monaural and binaural localization cues, but also frequency

composition of a sound stimulus. Notably, when the frequency composition of a sound is

restricted to a center frequency (CF) between 4 kHz and 12 kHz, localization of a sound

stimulus becomes impaired under binaural conditions (Musicant & Butler, 1984). There

is evidence to support the hypothesis that localization of narrow band sound is more

dependent upon the frequency composition and less dependent upon spatial location

(Musicant & Butler, 1984). Musicant and Butler surmised that the pinna modifications to

broadband sound serve to impart spatial referents, which are the cue to localization. Use

of narrow band sounds effectively isolate these spatial referents and the narrow band

sounds are associated with a specific location that appears to be independent of the actual

location of the sound source. In sum, the ability to localize broadband sound is a function

of binaural cues, the ITD and the ILD, and monaural spectral cues. The ability to localize

narrow band sound is most reasonably accounted for by the monaural spectral cues, and is less so by the location of the stimulus.

Cortical and Subcortical Structures of the Auditory System

Subcortical structures of the auditory system. Sound information is processed in a series of stages beginning within subcortical structures of the auditory system. First, the auditory nerve carries the sound information, synapsing onto the dorsal cochlear nucleus (DCN) and the ventral cochlear nucleus (VCN). From there, the information from the VCN bilaterally projects to the superior olivary nucleus (SON). From the DCN, information may project directly to the contralateral inferior colliculus. The information carried by the neurons from the DCN are likely the axons/pathway carrying the monaural spectral information. The SOC is the area in which binaural information converges (Masterton & Imig, 1984; Recanzone & Sutter, 2008). There are two components of the SON, 1) the lateral superior olive (LSO), and 2) the medial superior olive (MSO). From the SON, the information travels to the inferior colliculus (IC) and the superior colliculus (SC), located in the midbrain (Recanzone & Sutter, 2008). Lastly, the information projects from the brainstem to the medial geniculate in the thalamus. After the sound

information has traveled through the subcortical regions the sound information projects to the cerebral cortex.

Auditory cortex. The auditory cortex is located bilaterally in the temporal lobe. (Sweet, Dorph-Petersen, and Lewis, 2005). There is evidence to support an orderly arrangement, of frequency, in the auditory cortex, which is divided into three components: the core, the belt, and the parabelt (Chevillet, Riesenhuber, & Rauschecker, 2011; Kass and Hackett, 1999; 2000; Recanzone & Sutter, 2008; Wessinger, et al., 2001). The core area is located in the superior temporal gyrus (STG) and consists of the primary auditory receiving area (A1), the rostral field (R), and the rostral temporal field (RT). Further, the evidence suggests a tonotopic organization (neurons arranged by frequency from low to high) of the cochlea within the core area of the auditory cortex (Kikuchi, Horwitz, & Mishkin, 2010; Masterson & Imig, 1984). The belt field consists of the anterolateral (AL), mediolateral (ML) and caudolateral (CL) fields. There are eight field areas that hold specific representations for the cochlea (Kass & Hackett, 2000). The parabelt area is located laterally to the belt area and is divided into two sections, the caudal parabelt field and the rostral parabelt field (Recanzone & Sutter, 2008). Wessinger, et al. (2001) used functional magnetic resonance imaging (fMRI) to test how

well animal models of the lesser primates, demonstrating the core-belt-parabelt

arrangement of the auditory cortex, could be applied to the human auditory cortex. The

authors demonstrated that auditory information travels, hierarchically, in a core-belt-

parabelt fashion. Further, the authors discovered that pure tunes produced increased

activation levels in the core auditory area, a finding that was seen with direct neuronal

recordings in animals. An additional fMRI study demonstrated that pure tones activated

specific places within the core field, while broad spectral stimuli activated more

extensively throughout the auditory cortex, with heavy activity in the lateral belt field

(Rauschecker & Tian, 2000). More specifically, the AL, ML, and CL have demonstrated

a preference for broad spectral stimuli (Wessinger, et al; 2001). Recanzone and Sutter

(2008) suggest that the parabelt area is a likely candidate for processing complex features

of an auditory stimulus, such as location, as evidenced in both macaque and human

studies. Traditionally, the processing of auditory information has been viewed as solely

involving the temporal lobe; however, there is evidence supporting the involvement of

additional structures in the cortex that are utilized to garnish information concerning

features and location of the auditory stimulus.

The Auditory Dual-Pathway Model

The auditory "where" and "what" streams correspond to the visual system's

dorsal and ventral streams. In the visual system, the dorsal stream appears to be selective

toward identifying an object's location whereas the ventral stream appears to be selective

toward object identification. Recent evidence supports a similar finding in the auditory

system. Specifically, Rauschecker and Tian (2000) proposed that the auditory system has

two pathways, an anterior pathway and a posterior pathway. The authors demonstrated

two distinct divisions of the human cortical auditory system; two processing streams that

determine the "where" and "what" features of an auditory stimulus.

"Where" pathway. In monkeys it was demonstrated that neurons in the CL field of

the auditory cortex responded greatest to auditory **spatial** information (Kass & Hackett,

1999; Kass & Hackett, 2000; Rauschecker & Tian, 2000). A hierarchical pattern was seen

for both spatial information and monkey call (feature) information. First, auditory

information traveled to the core area, to A1. For spatial information, beginning with A1,

the information traveled to ML then to CL where neuronal sensitivity appeared to be the

greatest. In order to relate their findings to a human population, Rauschecker and Tian

(2000) conducted an fMRI study to investigate an auditory dual-pathway model in

humans, which the results tentatively confirmed. In particular, for auditory spatial

information, a pathway was seen beginning at the caudal portion of the supratemporal

plane and moving to areas within the inferior parietal lobe. Thus, based on the evidence,

spatial information travels from the temporal lobe to the parietal lobe. Utilizing fMRI,

Ahveninen et al. (2006) confirmed this organization in human subjects. Again, the where

pathway, from temporal lobe to parietal lobe, is involved in auditory spatial information.

Additionally, in a meta-analysis conducted by Arnott, et al. (2004), areas around the

superior frontal sulcus may be involved in localization, along with the inferior portion of

the parietal lobe and posterior portions of the temporal lobe. These findings suggest a

distinct pathway for auditory spatial information, which appears to involve both the

temporal and parietal lobes.

   "What" pathway. The identification of a "what" pathway in the auditory system has

focused primarily on monkey calls (MCs) or human vocal information. As such,

Rauschecker and Tian (2000) along with Kass and Hackett (1999 and 2000)

demonstrated an auditory "what" stream in monkeys utilizing MCs. They discovered that

when MCs are presented, beginning with A1, the selectivity for the stimulus increases as

it moves from ML to AL. Also, the selectivity increases from ML to CL. Rauschecker

and Tian (2000) demonstrated a similar pattern in humans, but with more specificity in the STG than was seen in the macaque. A meta-analysis conducted by Arnott, et al. (2004) showed that information concerning auditory recognition was processed in the anterior temporal lobe and the posterior temporal lobe. Further, involvement of the inferior frontal regions and the anterior temporal regions was seen when processing auditory recognition information. Ahveninen et al. (2006) demonstrated that the auditory recognition stream activates after the localization stream. The authors surmise that top-down processing is used in the auditory "what" stream, which results in a minimal delay in activation when compared with the activation of the "where" stream. Overall, the evidence supports a distinct path in which information concerning the identity of an auditory stimulus is processed in the temporal lobe.

The Cortical Mechanisms of Audition Utilizing Brain-Imaging Techniques

Brain imaging studies, such as electroencephalographic (EEG), magnetoencephalographic (MEG) and functional magnetic resonance imaging (fMRI) have expanded the understanding of specialized processes in the brain tied to processing auditory information. EEG and MEG studies have shown that the amplitude and the latency of the auditory N1m response is selectively tuned to spatial cues. A MEG study

conducted by Palomäki et al. (2000) demonstrated that contralateral and ipsilateral N1m

response was induced dependent upon perceived sound location. Further, the N1m

response showed a pronounced right-hemispheric bias, potentially marking the right

hemisphere as a key area for sound localization. Spatial cue selectivity, as indicated by

the N1m response, may be enhanced or diminished based on the amount of spatial cues

available (Palomäki et al, 2005). This response is more pronounced in the right

hemisphere of the brain, indicating an asymmetrical bias for sound localization. While

investigating the effects of attended and unattended sound stimuli, Tiitinen et al. (2006)

demonstrated that the N1m amplitude and P1m amplitude are sensitive to spatial cues,

while the P2m amplitude showed sensitivity in the presence of an auditory signal.

There is evidence supporting both ITD and IID differentially encode information in

the superior olivary complex (for review, see Grothe, Pecka & McAlpine, 2010) and

more recent studies have sought to determine whether these cues differentially encode in

cortical areas. Using dichotically presented clicks, Tardif et al. (2006) demonstrated

differential encoding of IID and ITD cues seen in inferior-frontal, temporal, and parietal

areas. Specifically, when measuring the N1 response, ITD cues were seen bilaterally

whereas responses to IID cues were restricted to the left hemisphere.

However, for simulated sound motion, Getzmann and Lewald (2010) discovered that both vertical and horizontal sounds shared the same cortical areas. The EEG study demonstrated that cortical responses, seen as N1 and P2 latencies, were the same for both vertical and horizontal stimulus types. These responses were seen bilaterally, and involved the premotor cortex, the superior parietal cortex, and inferotemporal cortex. In contrast, a MEG study conducted by Fujiki et al. (2002) showed differences in cortical processing of sounds by human listeners, utilizing monaural auditory cues and binaural auditory cues. According to the authors, binaural cues are processed 100 to 150 ms after sound onset while monaural cues are processed 200 to 250 ms following onset of a sound. The authors localized processing of monaural cues, more anterior to binaural cue processing, and to the right temporal cortex. Thus, processing of binaural and monaural cues may be processed differentially in the brain.

Present Study

The aforementioned evidence supports the notion that the auditory neural system has different levels of representation for sound information (Schreiner, Lead, & Sutter, 2000). The findings suggest that there are particular areas in the brain that are responsible for auditory spatial localization. However, the primary use of auditory broadband stimuli

makes it impossible to determine the brain's ability to localize narrowband sounds (those sounds which may explicate the role of monaural cues). To the best of our knowledge, little is known concerning the neural mechanisms underlying spatial auditory localization once spatial cues, particularly the ITD and ILD binaural cues, are made unavailable, such is the case with narrow band noise or for localization in the medial saggital plane, where the ITD and ILD cues are thought to result in a zero difference. The present study aims to inspect the N1 response for both narrow band and broadband sound in order to better understand auditory spatial localization. Further, we aim to extend our understanding of the parietal lobe as an additional area involved in the processing of spatial location when the auditory information is limited to narrow band noise. Specifically, we hope to address if narrowband sounds, the percept of spatial location that may not coincide with actual location, differ from what we see with broadband auditory stimuli. Also, the study aims to add to the existing understanding of the where/what pathways for sound localization and sound identification.

CHAPTER II

Method

Participants

Six undergraduate students (Age: $M = 23.6$, $SD = 3.2$; 2 women) were recruited.

All subjects were right handed. One subject was excluded for failing to fall within 20 dB

of audiometric zero on a standard hearing test. Also, due to the unknown consequences of

psychiatric and neurological disorders on EEG measurements concerning brain responses

to auditory stimuli, these populations were not included in the experiment. Subjects

provided informed written consent approved by the Middle Tennessee State University

Institutional Review Board.

Stimuli

Broadband noise stimuli were generated using CoolEdit Pro v1.2, signal

processing software. The bandwidth for the generated sound was filtered to include

frequencies from 200 Hz to 16 kHz with roughly equal sound levels across frequencies.

The sound was further filtered to compensate for the non-flat spectrum tied to

loudspeaker characteristics. Narrowband sounds were processed from another broadband

stimulus and were filtered to be 2 kHz wide with center frequencies of either 4 kHz or 10

kHz. These frequencies have spatial referents (Musicant & Butler, 1984) for low

elevations (4 kHz) and high elevations (10 kHz). All three stimuli had rise-fall times of

10msec and had cosine^2 onsets and offsets. Stimuli were 200msec in length. Further, the

stimuli were generated using a 44 kHz sampling frequency as this was required by the e-

prime software presentation system.

Design and Procedure

Subjects underwent a hearing test to determine if their hearing levels were within

20 dB of audiometric zero for tonal sounds between 250 Hz through 8000 Hz. For the

EEG/spatial testing subjects were fitted with a Geodesics Hydrocel Sensory Net® and

seated in a semi-anechoic chamber facing five vertical loud speakers. They were asked to

remain still throughout the task and limit eye blinks during trial presentation. Stimuli

were presented from five vertical loud speakers (one loudspeaker activated) at ±40°, ±20°

and 0°. All loudspeakers were located at 0° azimuth (straight ahead). Stimuli were

presented in three blocks with 150 stimuli per block. Within each block of trials, each

loudspeaker (5) was activated 10 times with each of the stimuli (3). The presentation

period for each sound was 2sec. in length with a 3sec. pause between each presentation.

This was necessitated by the need for mechanical switching, by the experimenter, of the

loudspeaker choice. The subjects' brain responses to the stimuli were recorded for 45

minutes. Following completion of the task, the subjects were carefully removed from the

semi- anechoic chamber and seated in a designated location. At that time, measurements

were taken with the Polhemus Patriot hardware© and the Locator software© in order to

create a 3D head model specific to each subject.

EEG Data Acquisition and Preprocessing.

The electroencephalogram (EEG) was recorded continuously from 128 electrodes

in a Geodesics Hydrocel Sensory Net® placed on the scalp with Cz at the vertex

connected to a NegAmps 300 amplifier. The vertical and horizontal electrooculograms

(EOG) were also recorded to detect both eye blinks and movements. The online data

were referenced to Cz, located at the top middle portion of the scalp. The frequency of

acquisition was 500Hz and impedances for each of the 128 electrodes were kept below

50kΩ. The EEG was filtered offline with a bandpass of 0.1 Hz to 100 Hz. The data

acquisition was controlled using the NetStation software and a MacBook Pro computer

version 10.00.

Net-Station Viewer and Waveform tools were used for preprocessing the EEG. Both

a 0.5 Hz low pass filter and a 100 Hz high pass filter were applied to the data. The data

were epoched from -500 to 500 ms relative to sound onset. Artifact rejection was performed, removing trials containing ocular artifacts and trials containing excessive noise. The average trials remaining per condition, out of 30 trials was 18.4 for a total average of 276 trials out of 450. Beginning with the broadband condition, the average amount of trials remaining for each speaker location is were follows: for the speaker located at +40 ° an average of 19 trials remained, for the speaker located at +20 °, the average amount of trials remaining was 20.4, the speaker located at 0 °, 17.4 trials remained, the speaker located at -20 °, 18.4 trials remained, and the speaker located at -40°, 16.6 trials remained. For the 4 kHz conditions, the average amount of trials per speaker location that remained were as follows: speaker located at +40° resulted in an average of 19.8 trials, speaker at +20° resulted in 18.6 trials, speaker at 0° resulted in 19.2 trials, for both the speaker at -20° and -40° an average of 20.4 trials remained. Lastly, the average trials remaining for the 10 kHz conditions, based on speaker location, were as follows: for the speaker located at +40°, 18.2 trials remained, for the speaker located at +20°, 18 trials remained, for the speaker at 0 °, 19.4 trials remained, for the speaker located at -20 °, 18.2 trials remained, and for the speaker located at -40 °, 16.2 trials remained. The epochs underwent baseline correction of 500ms prior to sound onset.

EEG Data Analysis

Time-frequency representation (TFR). Time-frequency analysis was conducted

using the Fieldtrip toolbox. TFRs were obtained by convolving the average waveform

with a Morlet wavelet. This resulted in a frequency resolution of sf = $f/6$ and a temporal

resolution of st = 1/sf, where f is the wavelet's center frequency, sf is the SD in for

frequency, and st is the SD for time. Wavelet convolutions were conducted between 8 Hz

and 50 Hz, with a frequency step of 1 Hz and a time step of 2 ms. Inter-individual

variability in absolute power was addressed by averaging the spectra of three speaker

conditions (-40°, 0°, and +40°) for each subject, resulting in a single value for each

frequency and each channel that serves as a baseline for normalizing the power spectra

for each condition and each subject.

Cluster-randomization analysis. Consistent trends in time-frequency cluster of

electrodes were identified with a cluster-randomization that was applied to the

normalized power spectra. This analysis, using cluster-based permutation tests, generates

paired comparisons between conditions. Power values were considered spatially

contiguous when they showed the same direction of effect, between a pair of adjacent

electrodes, thus identifying similar trends across successive time points. These

significance clusters were determined by performing multiple dependent t-tests between two conditions.

Three frequency bands, alpha (8 Hz – 12 Hz), beta (13 Hz – 29 Hz), and low gamma (30 Hz – 50 Hz), were formed from the division of the power spectra. The time windows of interest were between -500 and 500 ms. Two-tailed dependent t-tests were conducted on the power values generated from each time point and channel, derived by the comparisons made within a given frequency band for each subject. The sum of the t-statistics within each cluster was used to construct a cluster-level statistic. Data points were zeroed when they failed to exceed a significant level of *alpha* = .05. Grouping together non-zeroed adjacent points created clusters. The Monte Carlo method was used to compute the significant probability of the clusters. The Monte Carlo significant probability was formulated from the calculated proportion of clusters that were created from random data partitions, which resulted in larger test statistic than the clusters of the observed test statistic. Two speaker conditions, located at the highest point of elevation (+40°) and the lowest point of elevation (-40°) were compared in order to maximize our chances of finding significant differences.

Event related potential (ERP). ERPs were Cz referenced and the characterized auditory components N1 and P2 were identified. Auditory components were determined based on their expected latencies over regions of the scalp known for their maximum amplitude of auditory evoked potentials.

ANOVAs were performed on the mean amplitude of the ERP in the 50-150 ms latency range (N1) and 150-250 ms range (P2). The analysis was conducted by using a three-way repeated measure ANOVA with sound location (-40^0, 0^0, $+40^0$), sound type (4 kHz, 10 kHz, BB), and electrodes (128) as within-subject factors.

CHAPTER III

Results

Time-Frequency Representations

There were no differences seen in the activity between the spatial locations and the

sound conditions in any of the frequency bands used for the analyses. The alpha band, for

sound location at +40 degrees versus -40 degrees, resulted in marginally significant

findings for both the broadband condition ($p = .09$) and the 10K condition ($p = .09$).

Even-Related Potentials

Following sound onset, both a negative deflection (N1) and a positive deflection (P2)

were seen (See Figures 1, 2, and 3). For the N1 deflection, the three-way repeated

measures ANOVA revealed a significant main effect of sound type on N1 amplitudes, F

$(2, 8) = 8.63$, $p = .01$, *partial* $\omega^2 = .65$, indicating that differences between sound type

and N1 amplitudes can be predicted 65 percent of the time. However, post-hoc

comparison did not reveal any significant difference between the three sound types.

There was no significant main effect of speaker on N1 amplitudes, $F (1, 4) = .95$, $p = .38$,

partial $\omega^2 = .00$. Additionally, there was no significant interaction of sound location and

sound type on N1 amplitudes, $F (2, 8) = 1.51$, $p = .27$, *partial* $\omega^2 = .11$. The interaction

between sound type, location, and electrode on N1 amplitude was marginal, F (256, 1024) = 1.15, p = .07, *partial ω^2* = .04. Post-hoc comparison did not reveal any significant difference.

Concerning the P2 deflection, the three-way repeated measures ANOVA showed a significant main effect of sound type on P2 amplitudes, F (2, 8) = 22.27, p < 0.001, *partial ω^2* = .84. Post-hoc comparison did not reveal any significant difference. As with N1 amplitudes, there was no significant main effect of speaker on P2 amplitudes, F (1, 4) = 0.06, p = 0.81, *partial ω^2* = .00. There was no significant interaction between sound type and location on P2 amplitudes, F (2, 6) = 0.81, p = .48, *partial ω^2* = .49. Lastly, there was no significant interaction between sound location, sound type, and electrode on P2 amplitudes, F (256, 1024) = 0.55, p = 1.00, *partial ω^2* = .00.

CHAPTER IV

Discussion

The present study explored the neural mechanisms involved in sound localization

for vertical sources in the median sagittal plane. Both broadband and narrow band sounds

were investigated. We also aimed to extend current understanding of the parietal lobe's

involvement during sound localization. Our data analysis did not yield any clusters that

identified differences in neuronal processing across time for sound type over time.

Examination of auditory evoked responses did not reveal any differences in processing

location with sound identity in the primary auditory cortex for N1 and P2. However,

differences were discovered for sound type for both N1 and P2, indicating that, under

monaural conditions, narrow band and broadband sounds are differentially processed in

A1.

Parietal lobe and Sound Localization

The findings concerning involvement of the parietal lobe are in contrast to what

was expected based on the evidence in support of a dorsal and ventral auditory processing

stream. However, recent studies, utilizing EEG brain imaging techniques, have brought to

light new evidence, using more sophisticated designs, supporting the existence of a dorsal

and ventral auditory stream in human listeners. According to Ross and Tremblay (2009),

the P2 deflection represents feature evaluation of auditory signals, and is positioned more

anterior to the N1 deflection. Lewald and Getzmann (2011) investigated the possibility of

a dissociation of the N1 and P2 deflections, which would indicate differential processing

of auditory identity and auditory localization. The authors presented sounds originating

from horizontal locations, to human listeners. As with the current study, the authors

employed a free field passive listening paradigm to reduce any potential effects on the

EEG recording brought about by attention and/or arousal. Their findings suggest dual

involvement, separated by time, of auditory pathways for both spatial and feature specific

auditory information. The N1 deflection, which occurred 100 ms following stimulus

onset, demonstrated a distinct pathway that involved A1 and the dorsal pathway. The P2

deflection occurred 100 ms after the N1 deflection, and was localized to areas involving

the ventral pathway. In the present study, the possibility of a disassociation was not

specifically investigated. Further, we limited our investigation to sound elevation, which

relies on monaural/spectral cues, that may result in processing of auditory signals in more

anterior regions of the auditory system (Fujiki et al, 2002).

While the current study was unable to demonstrate involvement of additional auditory areas outside of the primary auditory cortex, Tiitinen et al. (2006) demonstrated little involvement of the parietal lobe and frontal areas during unattended auditory stimuli. Due to the passive nature of the present study, the auditory stimuli may have been unattended, thus leading to little involvement of the parietal lobe and additional auditory areas. Past research has relied on presenting stimuli along the horizontal plane, thus incorporating the use of binaural localization cues (ITD and ILD). Our study was restricted to elevation; thus it is unknown if horizontal and vertical sound localization rely on similar or distinct brain resources.

Limits of the Current Protocol and Future Directions

The present study employed both broadband and narrow band auditory stimuli while recent studies have used pure tones (Koiwa, Masaoka, Kusumi, & Homma, 2010), band pass filtered white noise (Lewald & Getzmann, 2011), animal sounds (Leavitt, Molholm, Gomez-Ramirez, & Foxe, 2011) and varying pitch sounds (De Santis, Clarke, & Murray, 2007) to investigate the dorsal and ventral auditory streams using EEG. Thus, the type of stimulus is inconsistent throughout the literature, and has not employed the utilization of two different sound types, as seen in the current study. The type of stimuli

and also trial presentation are inconsistent throughout the literature and ranged from 1920 (Lewald & Getzmann, 2011) to 240 (Koiwa et al., 2010). In the current study, the number of trials remaining for analysis purposes (an average of 276) was low in comparison to the more recently available studies.

Unlike the present study, and excluding the study conducted by Lewald and Getzmann (2011), studies produced by Koiwa et al. (2010) and Leavitt et al. (2011) utilized interactive listening tasks or a combination of passive and interactive listening paradigms. For instance, in the Koiwa et al. (2010) study, subjects listened to a sound, presented on either the left side or the right side of the listener, and were instructed to press a button, with either the left hand or the right hand, indicating which side the sound was presented. The study conducted by Leavitt et al. (2011) instructed subjects to identify a sound's location by drawing on a tablet the radial location in which the sound was projected. In the same study, during the "What" task, the subjects were instructed to identify the animal that produced a particular noise.

All of the more recent studies examining sound localization in relation to the dorsal and ventral streams have relied on presenting data along the azimuth (horizontal) plane. These studies have incorporated the use of all auditory cues, binaural (ITD and

ILD) and monaural cues. The current study presented elevated sound in the median

saggital plane, thus eliminating the use of binaural cues. To the best of our knowledge,

the current study is the only one of its kind to investigate elevated sound localization in

relation to the ventral auditory processing stream. Lacking, perhaps, in the number of

trials, in comparison to other studies, for analysis purposes, incorporating a passive

approach during the listening task, and utilizing only elevated sound presentation may

have produced results that make it impossible to determine if horizontal and vertical

sound localization involve separate or similar brain resources. Our future aim is to

incorporate a horizontal listening task, as well as integrate active listening, in which

participants will be requested to identify the location of an auditory stimulus. Also,

adding source electrode localization, in which a template based head model is used for a

distributed source analysis, will create a 3D picture detailing electrode positions. The 3D

picture will detail approximate electrode position in relation to cortical areas of the brain,

allowing for a more precise association between ERPs and the cortex.

Conclusion

By presenting elevated auditory stimuli, we could not confirm the use of different

or similar brain resources for horizontal and vertical sound localization. The study was

able to demonstrate differential neuronal processing of broadband and narrow band noise, but the extent of this processing could not be determined. We presented a novel approach to investigating the ventral processing stream by solely using monaural cues for sound localization, as well as utilizing three different sound stimuli.

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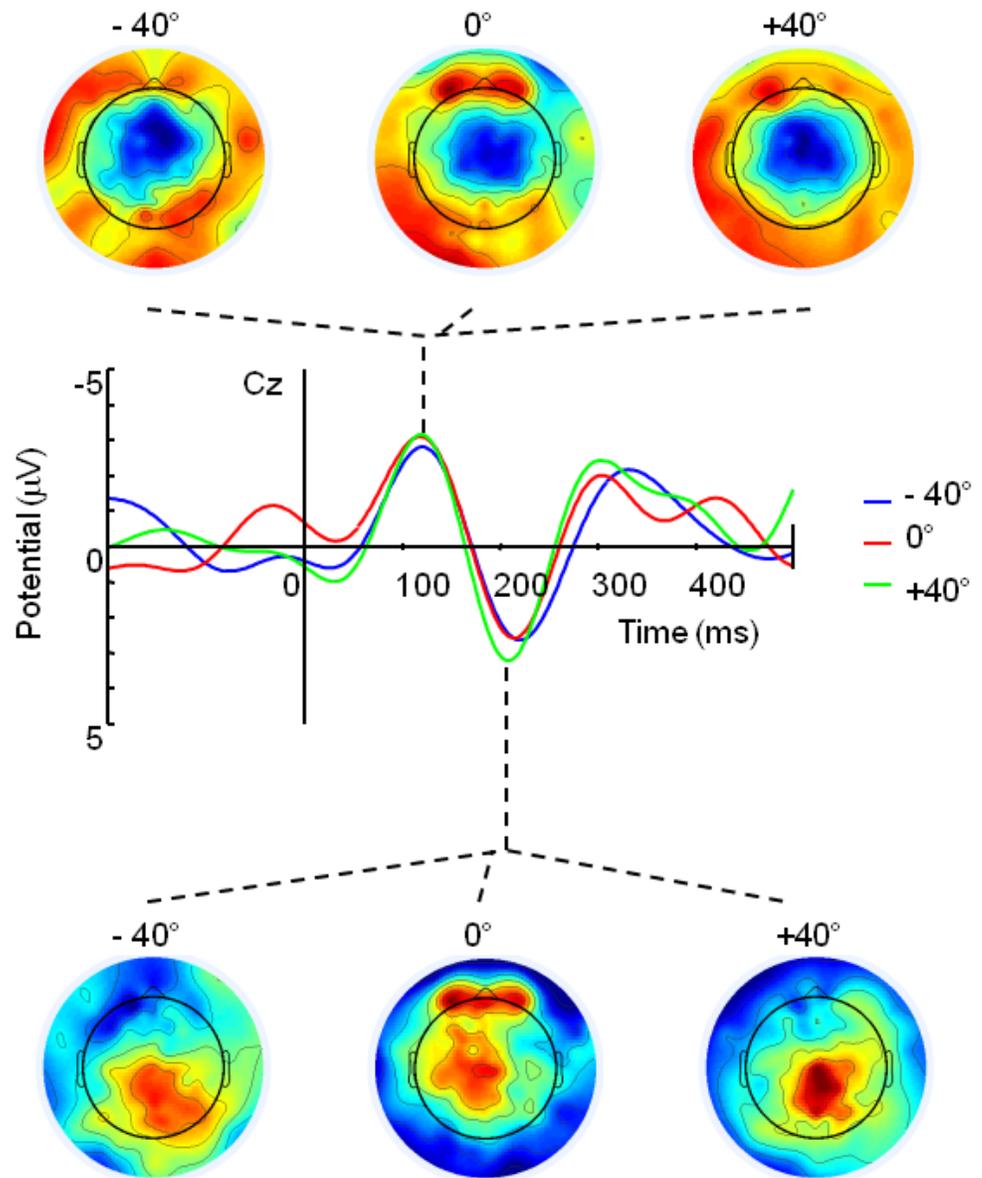
Figure 1: Electrophysiological Reponses for the 4k Condition. Middle row displays the ERPs recorded at an electrode located at the vertex (Cz) for the -40° (blue trace), 0° (red trace) and +40° (green trace) speaker positions. Top row represents the topographical maps of the N1 component at 120 ms for each speaker position. Bottom row represents the topographical maps of the P2 component at 212 ms for each speaker position.
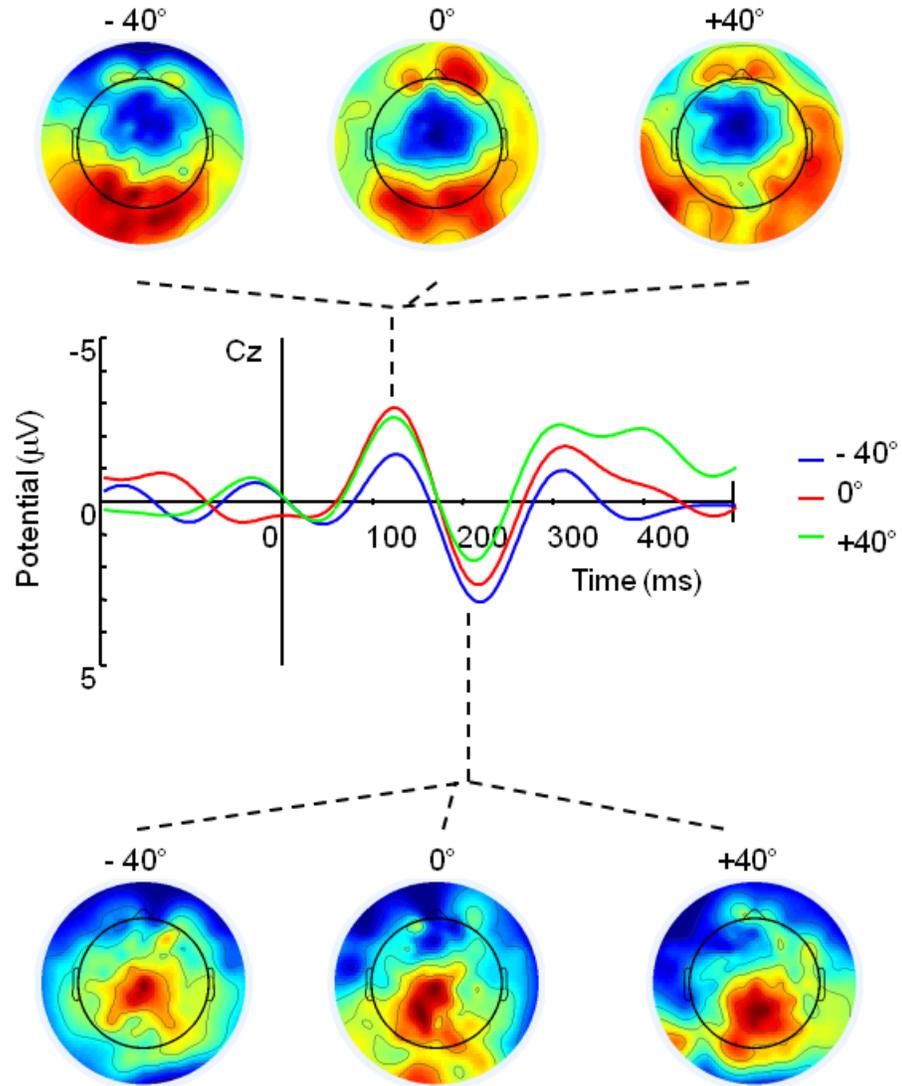
Figure 2: Electrophysiological Reponses for the 10k Condition. Middle row displays the ERPs recorded at an electrode located at the vertex (Cz) for the -40° (blue trace), 0° (red trace) and +40° (green trace) speaker positions. Top row represents the topographical maps of the N1 component at 120 ms for each speaker position. Bottom row represents the topographical maps of the P2 component at 212 ms for each speaker position.
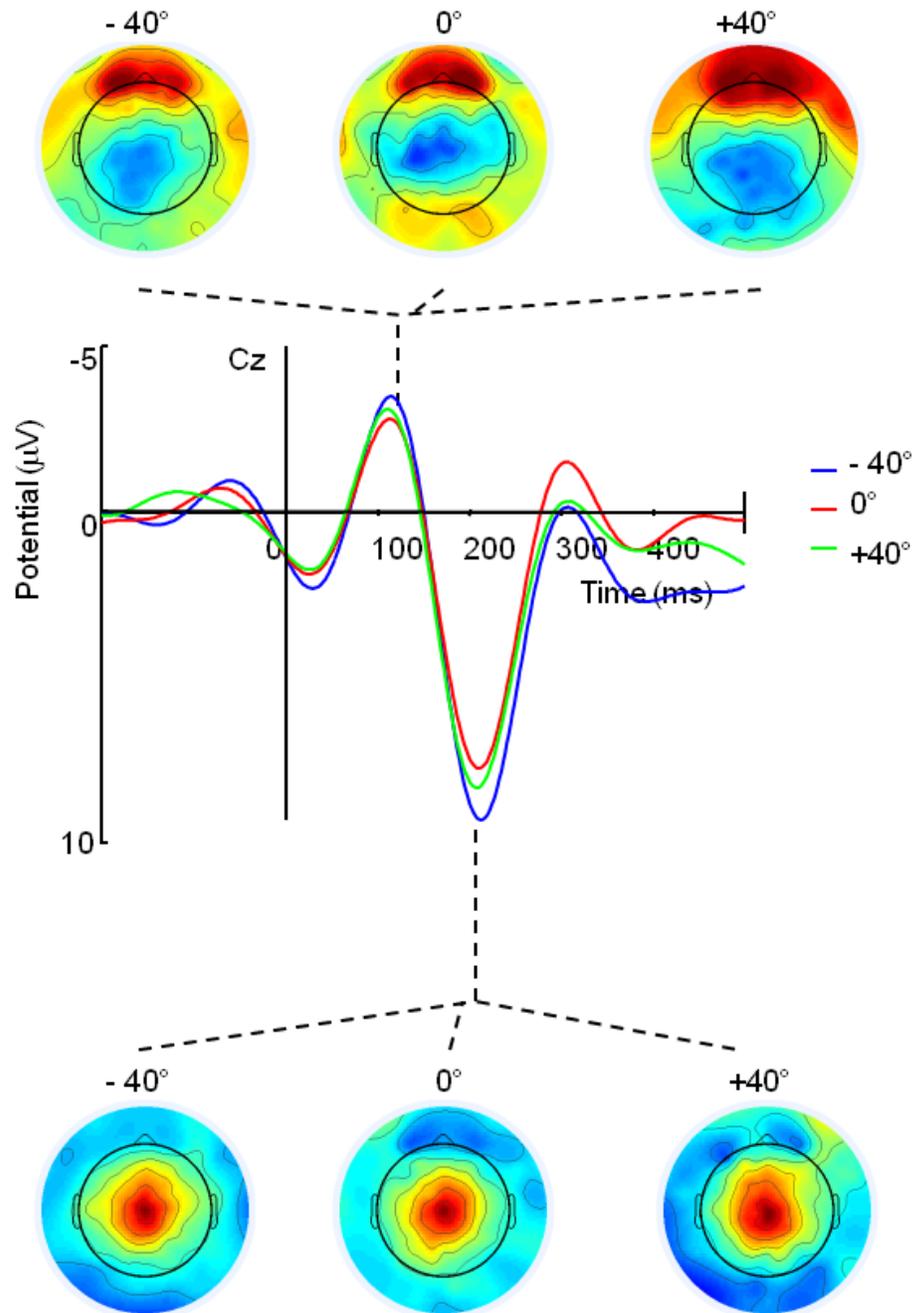
Figure 3: Electrophysiological Reponses for the broadband Condition. Middle row displays the ERPs recorded at an electrode located at the vertex (Cz) for the -40° (blue trace), 0° (red trace) and +40° (green trace) speaker positions. Top row represents the topographical maps of the N1 component at 120 ms for each speaker position. Bottom row represents the topographical maps of the P2 component at 212 ms for each speaker position.

APPENDIX

IRB Approval Letter

March 8, 2011
Protocol Number: 11-243
Protocol Title: "Neural Correlates of Broadband Width and Narrow Bandwidth Sound Localization"
Investigators: Alan Musicant, Cyrille Magne, Amanda Cumming
musicant@mtsu.edu, cmagne@mtsu.edu, aac3r@mtmail.mtsu.edu

Dear Investigator(s),

The MTSU Institutional Review Board, or a representative of the IRB, has reviewed the research proposal identified above. The MTSU IRB or its representative has determined that the study poses minimal risk to participants and qualifies for an expedited review under 45 CFR 46.110 Category 7.

Approval is granted for one (1) year from the date of this letter for **30** participants.

According to MTSU Policy, a researcher is defined as anyone who works with data or has contact with participants. Anyone meeting this definition needs to be listed on the protocol and needs to provide a certificate of training to the Office of Compliance. **If you add researchers to an approved project, please forward an updated list of researchers and their certificates of training to the Office of Compliance (c/o Emily Born, Box 134) before they begin to work on the project.** Any change to the protocol must be submitted to the IRB before implementing this change.

Please note that any unanticipated harms to participants or adverse events must be reported to the Office of Compliance at (615) 494-8918.

You will need to submit an end-of-project form to the Office of Compliance upon completion of your research located on the IRB website. Complete research means that you have finished collecting and analyzing data. **Should you not finish your research within the one (1) year period, you must submit a Progress Report and request a continuation prior to the expiration date.** Please allow time for review and requested revisions. Your study expires March 8, 2012.

Also, all research materials must be retained by the PI or faculty advisor (if the PI is a student) for at least three (3) years after study completion. Should you have any questions or need additional information, please do not hesitate to contact me.

Sincerely,

Emily Born
Compliance Officer
Middle Tennessee State University
eborn@mtsu.edu