Functional Brain Differences Predict Challenging Auditory Speech Comprehension in Older Adults

by

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ABSTRACT

Older adults often experience communication difficulties, including poorer comprehension of auditory speech when it contains complex sentence structures or occurs in noisy environments. Previous work has linked cognitive abilities and the engagement of domain-general cognitive resources, such as the cingulo-opercular and frontoparietal brain networks, in response to challenging speech. However, the degree to which these networks can support comprehension remains unclear. Furthermore, how hearing loss may be related to the cognitive resources recruited during challenging speech comprehension is unknown. This dissertation investigated how hearing, cognitive performance, and functional brain networks contribute to challenging auditory speech comprehension in older adults. Experiment 1 characterized how age and hearing loss modulate resting-state functional connectivity between Heschl’s gyrus and several sensory and cognitive brain networks. The results indicate that older adults exhibit decreased functional connectivity between Heschl’s gyrus and sensory and attention networks compared to younger adults. Within older adults, greater hearing loss was associated with increased functional connectivity between right Heschl’s gyrus and the cingulo-opercular and language networks. Experiments 2 and 3 investigated how hearing, working memory, attentional control, and fMRI measures predict comprehension of complex sentence structures and speech in noisy environments. Experiment 2 utilized resting-state functional magnetic resonance imaging (fMRI) and behavioral measures of working memory and attentional control. Experiment 3 used activation-based fMRI to examine the brain regions recruited in response to sentences with both complex structures and in noisy background environments as a function of hearing and cognitive abilities. The results suggest that working memory abilities and the functionality of the frontoparietal and language networks support the comprehension of speech in multi-speaker environments. Conversely, attentional control and the cingulo-opercular network were shown to support comprehension of complex sentence structures. Hearing loss was shown to decrease activation within right Heschl’s gyrus in response to all sentence conditions and increase activation within frontoparietal and cingulo-opercular regions. Hearing loss also was associated with poorer sentence comprehension in energetic, but not informational, masking. Together, these three experiments identify the unique contributions of cognition and brain networks that support challenging auditory speech comprehension in older adults, further probing how hearing loss affects these relationships.

DEDICATION

This dissertation is dedicated to the Phoenix volunteers who participated in this study. Without your commitment to research, this study would not have been possible.

This work is also dedicated to my mom. You used to tell me that I should become a lawyer since I loved to argue so much. Luckily, the science bug bit me first. Thank you for fostering in me the drive to pursue my passions.

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CHAPTER 1

INTRODUCTION

As many as one-third of older adults experience communication difficulties during everyday conversations (Committee on Hearing, Bioacoustics, and Biomechanics, 1988; Hamilton-Wentworth District Health Council, 1988). Many of these difficulties arise from needing to parse sentences with complex structures or while listening to speech in noisy background environments and are exacerbated by hearing loss (Caplan, DeDe, Waters, Michaud, & Tripodis, 2011; Humes, 1996; Kemtes & Kemper, 1997; Wingfield, Peelle, & Grossman, 2003). Such communication difficulties often lead to social isolation, depression, and anxiety, reducing overall quality of life (Ciorba, Bianchini, Pelucchi, & Pastore, 2012; Yorkston, Bourgeois, & Baylor, 2010). Current treatments largely rely on hearing aids, however, most older adults do not use hearing aids (Gopinath et al., 2011), resulting in a large proportion of older adults vulnerable to the negative effects of poor communication. Thus, the purpose of this dissertation was to investigate how hearing, cognitive abilities, and functional brain networks contribute to challenging auditory speech comprehension in older adults to identify possible intervention targets. In the following pages, three experiments are described that probe 1) how brain functional connectivity is affected by hearing loss, 2) how specific aspects of cognition and intrinsic connectivity of functional brain networks contribute to auditory speech comprehension, and 3) how activations of these networks in response to auditory speech comprehension are related to hearing and cognitive abilities.

One possible contributor to auditory speech comprehension deficits in older adults is hearing loss. By age 70, approximately two-thirds of adults have at least a mild hearing loss (Lin, Thorpe, Gordon-Salant, & Ferrucci, 2011). Previous work indicates that hearing loss negatively impacts auditory speech comprehension, particularly in noisy environments (Humes, 1996; Pichora-Fuller, 2003; Schneider, Daneman, & Pichora-Fuller, 2002). While there is a large body of literature characterizing cognitive and brain changes associated with age (for reviews see Grady, 2012; Salthouse, 2010), few studies have explored how hearing loss impacts the aging brain. Those that have report inconsistent structural brain changes, functional activation differences in response to auditory stimuli, and functional connectivity within Heschl’s gyrus (i.e.

primary auditory cortex) (see Cardin, 2016 for a review). However, it is unclear if Heschl’s gyrus is functionally connected to brain networks involved in cognitive and linguistic processing, and how this functional connectivity might be differentially affected by age and hearing loss. Thus, Experiment 1 aimed to first characterize how age and hearing loss uniquely impact the functional connectivity of Heschl’s gyrus to several well-studied brain networks.

Once controlling for hearing loss, studies suggest that individual cognitive abilities in older adults may also contribute to auditory speech comprehension abilities (Akeroyd, 2008; Humes, 2007). Regarding sentences with complex structures, previous work suggests that working memory performance is related to comprehension abilities in older adults (DeDe, 2014; Goral et al., 2011; Norman, Kemper, & Kynette, 1992). Comprehension of speech in noisy environments is proposed to be supported by attentional control, in addition to working memory (Rönnberg et al., 2013). The neural resources supporting aspects of working memory and attentional control have been previously ascribed to the frontoparietal and cingulo-opercular networks, respectively (Dosenbach et al., 2007; Marek & Dosenbach, 2018; Niendam et al., 2012; Petersen & Posner, 2012). Previous investigations into the brain regions recruited during auditory speech comprehension in older adults report increased activation in regions corresponding to the frontoparietal network in response to complex sentence structures (Peelle, Troiani, Wingfield, & Grossman, 2009; Tyler et al., 2009). Similarly, many studies of older adults report increased activation in brain regions corresponding to the cingulo-opercular network in response to speech in noisy environments (Eckert, Walczak, et al., 2008; Erb & Obleser, 2013; Vaden, Kuchinsky, Ahlstrom, Dubno, & Eckert, 2015). However, no study has examined the cognitive and neural resources that support both complex sentence structures and background noise in the same participants. Experiment 2 investigated how working memory, attentional control, and resting-state functional connectivity of the frontoparietal and cingulo-opercular networks predict comprehension of complex sentence structures and speech in noisy environments. This experiment uses resting-state fMRI to study these specific brain networks to avoid confounding effects related to performing a task.

To further understand the role of these cognitive and brain network resources in comprehension, it is also necessary to investigate how these brain networks respond (i.e. activate) during challenging auditory speech comprehension. Studies of speech comprehension in younger adults identify a fronto-parieto-temporal network (Friederici, 2012; Hickok & Poeppel, 2007; Rauschecker & Scott, 2009). When compared to younger adults, older adults have been shown to exhibit reduced activation within this typical speech comprehension network and recruit additional frontal and parietal regions outside of this network in response to challenging speech comprehension (Erb & Obleser, 2013; Peelle et al., 2009; Tyler et al., 2009; Vaden et al., 2015). However, previous work investigating the brain regions recruited in response to the effects of complex sentence structures and speech in noisy environments have only explored these effects independently. Thus, it is unknown if the cognitive resources recruited during these difficult comprehension conditions are in fact the same, or if they recruit distinct cognitive resources. Furthermore, very few studies have considered how hearing loss and cognitive abilities may affect the brain regions recruited in response to speech comprehension. Therefore, Experiment 3 examined within the same subjects the brain regions recruited in response to sentences with both complex structures and in noisy background environments, how the brain's response may differ by hearing and cognitive abilities, and if the activations of specific brain regions are predictive of comprehension abilities.

In summary, the purpose of the following experiments is to further our understanding of the major contributors to deficits in auditory speech comprehension in older adults. Specifically, this research attempts to tease apart the contributions of hearing loss, working memory, attentional control, and functional brain networks to speech comprehension. The goal of this work is to identify potential cognitive and brain network targets for future intervention that may aid in improving communication outcomes in older adults.

CHAPTER 2

EXPERIMENT 1: EFFECTS OF AGING AND AGE-RELATED HEARING LOSS ON HESCHL'S GYRUS AND BRAIN NETWORK FUNCTIONAL CONNECTIVITY

Introduction

Beginning at age 50, as many as 15% of adults in the United States have at least a mild hearing loss, with this rate doubling every decade such that by the seventh decade approximately two-thirds of adults have a hearing loss (Lin, Thorpe, et al., 2011). These trends reflect hearing thresholds typically greater than 25 dB and assessed between .5 and 4 kHz, wherein most of the frequencies of speech sounds fall. However, the prevalence of high-frequency hearing loss (thresholds between 4 and 8 kHz) is much greater at an earlier age, affecting one-third of adults 50-59 years and 59% of adults 60-69 years (Agrawal, Platz, & Niparko, 2008). These changes in hearing abilities in older adults negatively impact communication, resulting in speech comprehension difficulties, particularly in noisy environments (Desjardins & Doherty, 2013; Moore et al., 2014; Tun, Benichov, & Wingfield, 2010). However, it is unclear if these difficulties are driven by peripheral hearing loss (i.e. changes within middle or inner ear structures, particularly the cochlea), central hearing loss (i.e. changes within the vestibulocochlear cranial nerve, brain stem, or cortex), or both (Humes, 2008). Hearing loss is further linked to declines in self-reported activities of daily living and overall quality of life (Ciorba et al., 2012; Dalton et al., 2003; Hawkins et al., 2012). While hearing aids are the most common treatment for managing age-related hearing loss, only about 40% of adults over 70 years old with a hearing loss use hearing aids due to high costs and perceived lack of need (Gopinath et al., 2011; Lin, Thorpe, et al., 2011). Thus, given the high prevalence of adults with age-related hearing loss, most of whom do not seek treatment, there is a rapidly expanding population of older adults living with the effects of hearing loss and it is critical that the effects of hearing loss in the aging brain are thoroughly characterized to identify potential areas of intervention.

Recent work has linked age-related hearing loss to a roughly two-fold increased risk for cognitive decline and dementia, with hearing loss likely preceding the onset of cognitive decline by five to 10 years (Albers et al., 2015; Loughrey, Kelly, Kelley, Brennan, & Lawlor, 2017). In a large meta-analysis of the association between age-related hearing loss and cognitive abilities by Loughrey et al. (2017), the authors report small but significant declines in cognition with hearing loss across all 10 tested cognitive domains, including global cognition, executive functions, episodic memory, processing speed, semantic memory, and visuospatial ability. While the causal relationship between age-related hearing loss and declines in cognitive abilities are not well understood, two possible mechanisms have been proposed: (1) both conditions derive from a common etiology or (2) sensory deprivation (i.e. hearing loss) may lead to cognitive decline (Baltes & Lindenberger, 1997; Lin, Metter, et al., 2011). This growing body of literature characterizing the high prevalence of hearing loss and its link to cognitive decline points to a need to uncover how hearing loss impacts the brain separate from other effects of aging.

Few studies have investigated how age-related hearing loss impacts the brain (for a review see Cardin, 2016). Changes to brain structure related to age-related hearing loss are unclear: some studies report gray matter volume decreases associated with hearing loss in primary auditory cortex (i.e. Heschl’s gyrus) and other temporal lobe structures (Eckert, Cute, Vaden, Kuchinsky, & Dubno, 2012; Husain et al., 2011; Peelle, Troiani, Grossman, & Wingfield, 2011), while others report volume increases within Heschl’s gyrus and the superior and middle temporal gyri (Boyen, Langers, de Kleine, & van Dijk, 2013). One potential reason for this discrepancy in findings regarding Heschl’s gyrus volume and hearing loss is that specific subdivisions of Heschl’s gyrus have been shown to be differentially impacted by the range of hearing loss, with high-frequency hearing loss exhibiting lower gray matter volume in the Te1.0 region and low-frequency hearing loss correlating with lower volume in the Te1.2 region (Eckert et al., 2012). The discrepancies also may be due to differences in how primary auditory regions are anatomically defined (e.g. cytoarchitectonic divisions of Heschl’s gyrus compared to averaging across the entire gyrus) and how hearing thresholds are defined (e.g. averaged over all tested frequencies or only the higher frequencies predominately impacted by age) (Cardin, 2016). Across the entire brain, a longitudinal study of older adults (aged 56-86) that compared gray matter volume reported no volume differences at baseline between the group with hearing loss compared to the normal hearing group, but at the follow up six years later, those with a hearing loss exhibited accelerated volume declines, particularly within the right temporal lobe (Lin et al., 2014).

Functional MRI (fMRI) has identified differences in brain activation between older adults with and without hearing loss in response to auditory stimuli. In a study utilizing tones, activation was negatively correlated with hearing thresholds, such that there was reduced activation in subcortical auditory regions with increasing hearing loss, but no relationship with activation in auditory cortex (i.e. bilateral Heschl's gyri and superior temporal gyri) (Boyen, de Kleine, van Dijk, & Langers, 2014). Conversely, fMRI activation to more complex auditory stimuli, like sentences of varying syntactic complexity, is reduced within Heschl's gyrus (Te1.0 and Te1.1) in adults with poor hearing, even after controlling for age (Peelle et al., 2011). However, other studies report no difference in fMRI activation within Heschl's gyrus and superior temporal regions in response to tones or words with age-related hearing loss (Harris, Dubno, Keren, Ahlstrom, & Eckert, 2009; Profant et al., 2015). Hearing-related differences in temporal regions also have been identified using high-density electroencephalography (EEG) and cortical auditory evoked potentials: adults with hearing loss show increased amplitude and latency in the P2 peak, which is postulated to originate from Heschl's gyrus, as well as reduced activation in temporal regions and increased activation in frontal areas (J. Campbell & Sharma, 2013; Lightfoot, 2016). However, it is unclear how the changes in structural and functional brain measures associated with age-related hearing loss relate to well-studied changes associated with age alone.

There is a much larger body of literature investigating age-related changes to the brain without considering any effects of hearing loss. These studies report gray matter volume and thickness decreases prominently within prefrontal cortical regions, with temporal cortex expressing more moderate declines, and smaller declines in parietal and occipital lobes (Alexander et al., 2006; Fjell et al., 2009; Raz & Rodrigue, 2006; Walhovd et al., 2005). Studies of age-related differences in fMRI activation in a variety of tasks reveal that older adults exhibit activation in brain regions not recruited by younger adults and overactivation compared to younger adults in shared regions (see Grady, 2012 for a comprehensive review). In response to complex sentence stimuli, older adults showed decreased activation in left inferior frontal regions compared to younger adults and additional recruitment of middle and superior frontal regions not observed in younger adults (Peelle et al., 2009). When listening to speech presented in background noise, older adults showed reduced activation in auditory cortex near Heschl's gyrus, and increased activation in frontal and parietal regions (Wong et al., 2009). However, these activations in response to auditory language processing are likely impacted by hearing loss, so again it is difficult to know how much age-related hearing loss is driving these effects.

Resting-state fMRI can be used to disentangle general age effects from the effects of age-related hearing loss on brain function. This technique measures functional connectivity of brain networks in the absence of any task, avoiding introducing task- or stimuli-related confounds, yet still capturing the brain networks that are modulated during cognitive tasks (Calhoun, Kiehl, & Pearlson, 2008; Smith et al., 2009). Resting-state fMRI investigates activity within and between specific brain regions and entire brain networks via measures of functional connectivity (i.e. correlations between intrinsic activation patterns of anatomically distinct brain regions) (van den Heuvel & Hulshoff Pol, 2010). Studies of resting-state fMRI changes with age report that older adults have less distinct brain networks, as reflected in decreased within-network connectivity and increased between-network connectivity (Geerligs, Maurits, Renken, & Lorist, 2014; Geerligs, Renken, Saliasi, Maurits, & Lorist, 2015; Tomasi & Volkow, 2012). Many studies report age-related declines in resting-state fMRI activity predominately within the default mode network (Andrews-Hanna et al., 2007; K. Campbell, Grigg, Saverino, Churchill, & Grady, 2013; Damoiseaux et al., 2008; Tomasi & Volkow, 2012; Vidal-Piñeiro et al., 2014), as well as other networks including the motor, dorsal attention, and salience networks (Allen et al., 2011; Onoda, Ishihara, & Yamaguchi, 2012; Tomasi & Volkow, 2012). One study demonstrated that functional connectivity between the salience network and auditory networks declined with age (Onoda et al., 2012). However, none of these studies accounted for participant hearing abilities. The few studies investigating hearing loss using resting-state fMRI report that the extent of an auditory network, defined by the functional connectivity from both left and right Heschl's gyrus, did not differ between middle-aged normal and impaired hearing groups; however, those with hearing loss exhibited altered connectivity of the dorsal attention and default mode networks compared to those with normal hearing (Husain, Carpenter-Thompson, & Schmidt, 2014; Schmidt, Akrofi, Carpenter-Thompson, & Husain, 2013). There also is evidence to suggest that age-related hearing loss is linked to increased coupling of visual and auditory processing, based on a positive relationship between hearing loss and functional connectivity between right visual area MT+ and left Heschl's gyrus (Puschmann & Thiel, 2017). With the significant overlap in the brain networks found to be affected by age in general and age-related hearing loss in particular, it is unclear what effects can be independently attributed to hearing loss versus other aspects in aging.

Given the large prevalence of hearing loss in older adults and its impact on communication and daily life, it is critical that studies characterize the impact of age-related hearing loss on the brain and compare these to brain changes associated with age alone. Heschl's gyrus is a key target in investigating the effects of hearing loss due to its role in auditory processing and the conflicting findings regarding the structural and functional impact of hearing. The structural and effective connectivity of Heschl's gyrus to nearby temporal auditory processing regions has been explored in humans (Brugge, Volkov, Garell, Reale, & Howard, 2003; Tardif & Clarke, 2001; Upadhyay et al., 2008). However, the functional connectivity pattern from Heschl's gyrus to other cortical regions is relatively unknown. One study determined that Heschl's gyrus was functionally connected to the calcarine fissure of the visual cortex in younger adults (Eckert, Kamdar, et al., 2008). This mirrors anatomical tracer studies of nonhuman primates which reveal projections between auditory and visual cortices (Rockland & Ojima, 2003). Critically, it is unknown if Heschl's gyrus is functionally connected to other brain networks involved in higher-order cognitive processing (e.g. salience or default mode networks) and how this connectivity pattern might differ as a function age and of age-related hearing loss. Therefore, the current study aims to characterize functional connectivity between Heschl's gyrus and cognitive brain networks in a group of younger adults and a group of older adults, and to determine the impact of age-related hearing loss on functional connectivity. Resting-state fMRI methods were used to explore brain networks instead of task-based fMRI methodologies because resting-state fMRI allows us to avoid individual differences in performance or interpretation of task directions, which can be challenging for older adults, nor does it rely upon sufficient perception of auditory stimuli, which could be confounded by participant hearing status.

In the present study functional connectivity was characterized from left and right Heschl's gyrus to several well-studied cognitive networks implicated in studies of both age and age-related hearing loss (language, cingulo-opercular, default mode, dorsal attention, visual, and sensorimotor networks) in older and younger adults. I collected the older adults' resting-state fMRI data and the younger adults' data was obtained from the Human Connectome Project (Van Essen et al., 2013). The goal of the analysis in young adults was to identify the functional connectivity of Heschl's gyri prior to age-related changes to serve as a baseline or comparison with the older adults; to my knowledge functional connectivity between Heschl's gyrus and cognitive networks has not yet been investigated in young adults. In the group of older adults, functional connectivity was computed between each hemisphere's Heschl's gyrus to each cognitive network of interest (language, cingulo-opercular, default mode, dorsal attention, visual, and sensorimotor networks) and correlated with participant hearing levels, controlling for age, to determine if hearing loss is related to changes in brain functional connectivity that are distinct from age-related changes. Given the findings of previous literature, it was predicted that age-related hearing loss would be associated with increases in functional connectivity between Heschl's gyrus and the language, cingulo-opercular, and visual networks, possibly as mechanisms of auditory compensation. Further, this study aimed to identify age-related differences in functional connectivity between the two groups. It was expected that decreases in functional connectivity between Heschl's gyri and all tested networks in the older adults compared to the younger adults would be observed, coinciding with previous findings of age-related functional connectivity declines within and between cognitive brain networks.

Methods

Older adults

The older adult group consisted of 31 adults aged 60 to 80 years (20 women; mean(sd) age=67.8(5.6) years, mean(sd) education=17.5(3.3) years) recruited from the greater Phoenix area. All participants were native English-speaking, right-handed as determined by the Edinburgh Handedness Inventory (mean(sd)=94.6(16.2)), and free from dementia, as determined by the Mini Mental Status Exam, score ≥27 (mean(sd) = 29.1(1.0), range 27-30). No participant expressed indications of depression, as measured by the 15-item Geriatric Depression Scale where a score greater than five suggests depression (mean(sd)=0.9±1.0, range 0-5). Written informed consent was obtained from each participant in accordance with Arizona State University's Institutional Review Board and the US Federal Policy for the Protection of Human Subjects guidelines. Participants received a small monetary compensation for their efforts.

Pure-tone audiometry assessed participant hearing ability in both ears and was conducted using a GSI 18 Audiometer and supra-aural headphones. The following frequencies were tested: .250, .500, 1, 2, 4, and 8 kHz. If the participant wore hearing aids, hearing acuity was evaluated unaided. MRI was also conducted unaided. Hearing ability was summarized as the average threshold between all tested frequencies over both ears, where a higher threshold indicates greater hearing loss (mean(sd)=26.76(12.01) dB, range = 6.25 – 52.92 dB; Figure 1). Hearing ability did not significantly correlate with participant age (*r*=0.320, *p*=0.080) or MMSE scores (*r* =.-.029, *p*=0.875). MMSE scores also did not significantly correlate with participant age (*r*=-.068, *p*=0.717).

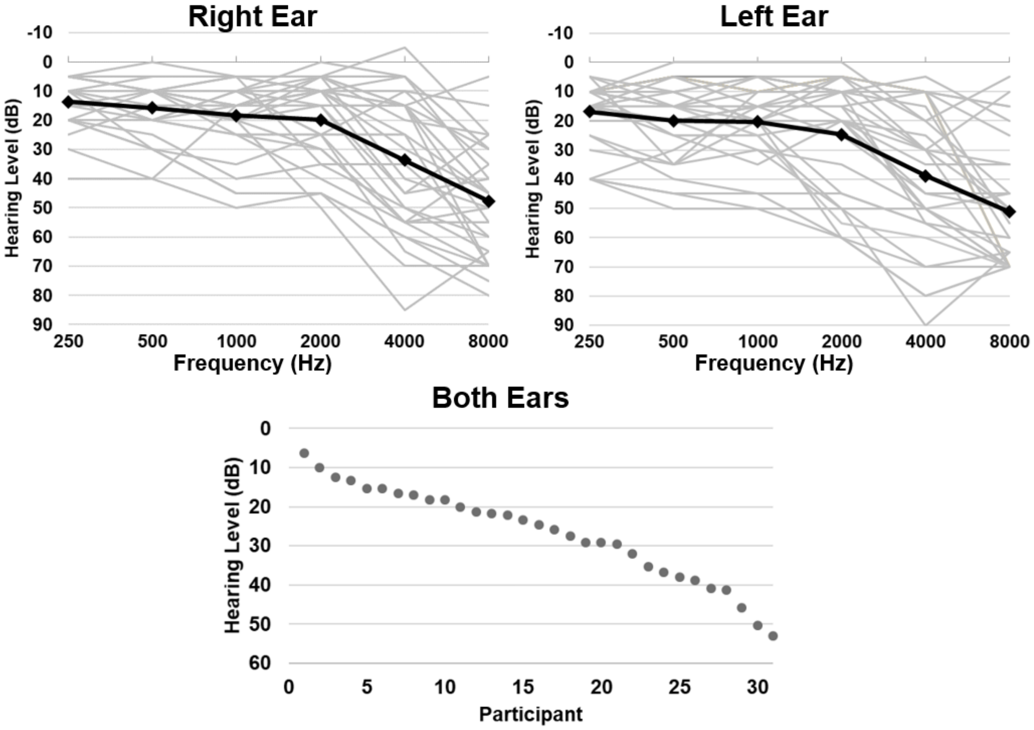

Figure 1. Hearing thresholds for the older adult group as assessed by pure-tone audiometry. Top left and right panels depict average thresholds for each ear. Individual participant thresholds are shown in light gray, with group average thresholds shown in black. Bottom panel depicts the average of the thresholds across frequencies for both ears per participant, depicting a range of normal hearing to a moderate hearing loss in the older adult group.

MRI scanning of the older adults was conducted at the Barrow Neurological Institute in Phoenix, AZ on a research-dedicated 3T Phillips Ingenia scanner. During the resting-state fMRI acquisition, participants lay awake, in the absence of an explicit task, with eyes open and fixed on a crosshair. Resting-state fMRI data were collected using single-shot EPI with ADNI 3 imaging parameters (Weiner et al., 2017): one 10-minute run, TR=3000ms, TE=30ms, flip angle=90°, FOV=217x217, matrix=64x62, 48 axial slices, 3.39mm slice thickness, in-plane resolution=3.39x3.39mm. Field maps were also collected to account for field inhomogeneity using the following parameters: TR=20ms, TE (short)=2.3ms, TE (long)=4.6ms, flip angle=10°, FOV=240x240, matrix=80x80, voxel size=3x3x3mm, 52 sagittal slices, acquisition time =1 minute 22 seconds. A T1 MPRAGE anatomical scan also was acquired for each participant with the following parameters: TR=6.74s, TE=3.10ms, flip angle=9°, FOV=270x253, matrix=256x256, voxel size=1.1x1.1x1.2mm, 170 sagittal slices, acquisition time=5 minutes 34 seconds.

Field maps were created using SPM12's FieldMap toolbox and applied to the pre-processing pipeline to correct for field inhomogeneities within the resting-state functional images. The following pre-processing procedures for the older adult group were conducted in the Functional Connectivity Toolbox (CONN; Whitfield-Gabrieli and Nieto-Castanon, 2012) using SPM12 functions: field map correction, slice-timing correction, realignment, coregistration to each participant's anatomical scan, normalization to the MNI template, and spatial smoothing with an 8mm FWHM Gaussian kernel. These procedures represent the standard preprocessing stream offered in the CONN toolbox and are very similar to the preprocessing of the HCP data of the younger adults, described below.

Younger adults

The younger adults' data were obtained from the 100 Unrelated Subjects data cohort of the WU-Minn Human Connectome Project (HCP) consortium (Van Essen et al., 2013). Thirty-one adults matched to the gender distribution of the older adult group (i.e. 20 women) between the ages of 22 and 35 years (the HCP provides an age range, not exact ages of participants) were selected for use in the present study. All younger adults were cognitively normal, as determined by the MMSE results provided by the HCP (mean(sd) = 29.0(1.1), range 26-30). Hearing abilities are not provided in the HCP dataset.

Preprocessed data from two, 15-minute resting-state fMRI runs were used in this study and were acquired on a 3T Seimens Skyra scanner with the following imaging parameters: TR=720 ms; TE=33.1 ms; FOV=208×180 mm^2; number of slices=72; and voxel resolution=2.0×2.0×2.0 mm^3 (Glasser et al., 2013; S. M. Smith et al., 2013). The data were preprocessed by the HCP using the "minimal processing pipeline scripts" as outlined by Glasser et al. (2013) which include steps for field map correction, realignment, coregistration to the anatomical scan, and normalization to the MNI template, similar to the steps applied in the older adult group. Spatial smoothing was also applied with an 8mm FWHM Gaussian kernel to mirror the preprocessing applied to the older adult group.

Functional connectivity analysis

Processing and analysis of the resting-state functional neuroimaging data was conducted using standard pipelines within CONN. For each participant, denoising was performed to remove potentially confounding effects including participant motion, physiological signals, outlier images (using the aCompCor strategy (Behzadi, Restom, Liau, & Liu, 2007; Chai, Castañón, Öngür, & Whitfield-Gabrieli, 2012)), and bandpass filtering. Within each age group, functional connectivity was computed between the anatomical ROIs (regions of interest) of left and right Heschl's gyrus (centers of mass 46 -17 7 and -45 -20 7, respectively) and ROIs within the following networks: default mode network, sensorimotor network, visual network, cingulo-opercular network (i.e. bilateral insulae and dorsal anterior cingulate of the salience network), dorsal attention network, and language network (see Table 1 for a list of network regions and coordinates and Appendix A, Figure A1 for overlays of each networks' ROIs on a template brain). Network ROIs were pre-defined in CONN and were derived from an independent component analysis of 497 subjects from the HCP (Whitfield-Gabrieli, 2012). For each participant and each ROI, the time course was averaged across all voxels within the ROI. A bivariate correlation was computed between the average time courses of each ROI and Fisher Z-transformed (i.e. ROI-to-ROI connectivity).

Table 1. Network and ROI names and MNI center of mass coordinates

	X	Y	Z
Default Mode Network			
Medial Prefrontal Cortex (MPFC)	1	55	-3
L Lateral Parietal (LP)	-39	-77	33
R Lateral Parietal (LP)	47	-67	29
Precuneus Cortex (PCC)	1	-61	38
Sensorimotor Network			
L Lateral	-55	-12	29
R Lateral	56	-10	29
Superior	0	-31	67
Visual Network			
Medial	2	-79	12
Occipital	0	-93	-4
L Lateral	-37	-79	10
R Lateral	38	-72	13

Cingulo-opercular Network			
Anterior Cingulate Cortex (ACC)	0	22	35
L Anterior Insula	-44	13	1
R Anterior Insula	47	14	0
Dorsal Attention Network			
L Frontal Eye Fields (FEF)	-27	-9	64
R Frontal Eye Fields (FEF)	30	-6	64
L Intraparietal Sulcus (IPS)	-39	-43	52
R Intraparietal Sulcus (IPS)	39	-42	54
Language Network			
L Inferior Frontal Gyrus (IFG)	-51	26	2
R Inferior Frontal Gyrus (IFG)	54	28	1
L Posterior Superior Temporal Gyrus (pSTG)	-57	-47	15
R Posterior Superior Temporal Gyrus (pSTG)	59	-42	13

To characterize, within each group, the average connectivity from left and right Heschl's gyrus to the contralateral Heschl's gyrus and to each network ROI, ROI-to-ROI connectivity was assessed using one-sample t-tests threshold at $p<0.05$ FDR. Next, ROI-to-ROI connectivity was compared between age groups using independent samples t-tests (two-tailed, $p<0.002$ with Bonferroni corrections (0.05/22=.002) for the 22 network ROIs). Previous studies have made comparisons between groups whose resting-state fMRI data were acquired by different scanners, with different parameters, and/or with slightly different seeds, and high reliability was found for seed-based connectivity analyses such as the ones conducted here (Hong, Park, Cho, & Park, 2017; Noble et al., 2017; Yamashita et al., 2018; Yang et al., 2013).

To compare changes in connectivity associated with hearing loss to that of age, the following analyses were conducted within the older adult group: 1) hearing ability was correlated with the connectivity between both left and right Heschl's gyri to each network ROI, controlling for age ($p<0.05$, FDR corrected), and 2) participant age was correlated with connectivity between both left and right Heschl's gyri to each network ROI, controlling for hearing loss, ($p<0.05$, FDR corrected).

Results

Heschl's gyrus connectivity within each age group

For the younger adult group, the average functional connectivities from left and right Heschl's gyrus to ROIs within each brain network are characterized in Figures 2 and 3, respectively, and Table 2. A one-sample t-test revealed that left Heschl's gyrus was significantly and positively connected to the contralateral Heschl's gyrus and all ROIs within the dorsal attention, language, cingulo-opercular, and sensorimotor networks, and all but one ROI (the occipital) of the visual network, ($p<0.001$). Left Heschl's gyrus was also positively connected to the posterior cingulate and bilateral parietal ROIs of the default mode network ($p<0.028$). The pattern of connectivity from right Heschl's gyrus to each network mirrored the pattern of connectivity in left Heschl's gyrus for all ROIs ($p<0.001$) except for the ROIs of the default mode network, which were not significant.

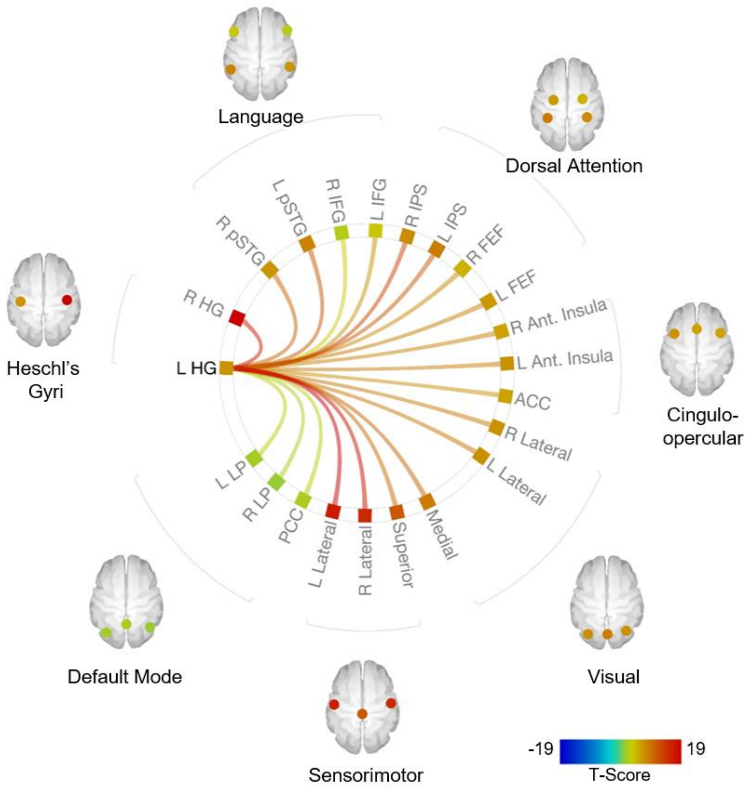

Figure 2. Functional connectivity between left Heschl's gyrus and several brain networks in the younger adult group, $p<0.05$, FDR. Line colors reflect the T-score with warmer colors reflecting larger, positive T-scores.

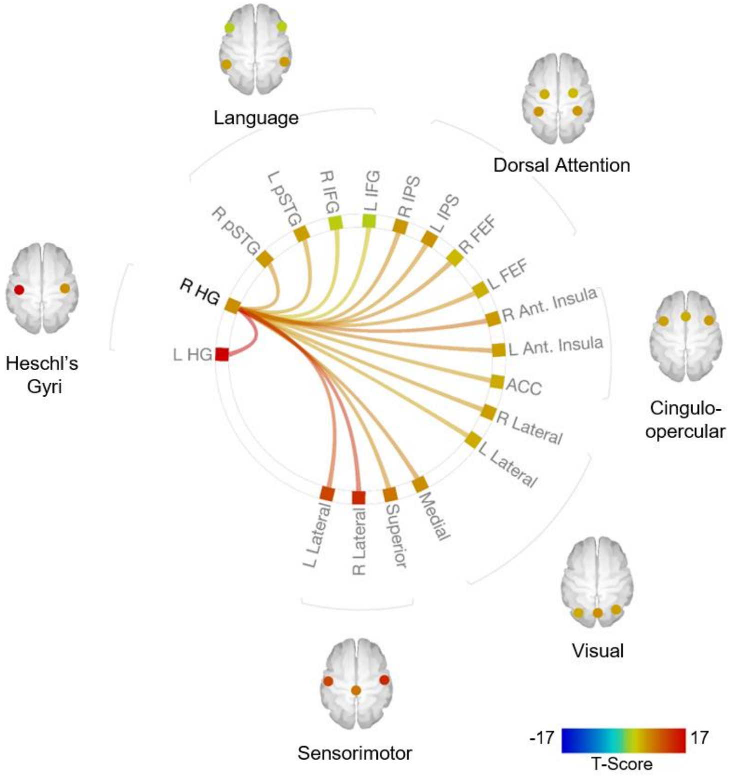

Figure 3. Functional connectivity between right Heschl's gyrus and several brain networks in the younger adult group, $p<0.05$, FDR. Line colors reflect the T-score with warmer colors reflecting larger, positive T-scores.

Table 2. ROI-to-ROI functional connectivity from Heschl's gyrus to network ROIs within younger adult group

ROI (Network)	T-value	*p* value
Left Heschl's Gyrus		
L Lateral (Sensorimotor)	19.84	<0.001
R Lateral (Sensorimotor)	18.45	<0.001
R Heschl's Gyrus	17.81	<0.001
R IPS (Dorsal Attention)	13.48	<0.001
L IPS (Dorsal Attention)	12.17	<0.001
L pSTG (Language)	11.83	<0.001
R pSTG (Language)	11.30	<0.001
Medial (Visual)	10.99	<0.001
Superior (Sensorimotor)	10.63	<0.001
L Lateral (Visual)	9.78	<0.001
R Lateral (Visual)	9.51	<0.001
L Anterior Insula (Cingulo-opercular)	9.26	<0.001
L FEF (Dorsal Attention)	9.03	<0.001
R Anterior Insula (Cingulo-opercular)	8.84	<0.001
R FEF (Dorsal Attention)	8.47	<0.001
ACC (Cingulo-opercular)	7.64	<0.001
L IFG (Language)	7.57	<0.001
R IFG (Language)	3.90	<0.001
L LP (Default Mode)	3.44	0.002

PCC (Default Mode)	3.41	0.002
R LP (Default Mode)	2.44	0.028
Right Heschl’s Gyrus		
L Heschl’s Gyrus	17.81	<0.001
R Lateral (Sensorimotor)	14.36	<0.001
L Lateral (Sensorimotor)	12.05	<0.001
R Anterior Insula (Cingulo-opercular)	10.27	<0.001
Medial (Visual)	8.65	<0.001
L Anterior Insula (Cingulo-opercular)	8.54	<0.001
R FEF (Dorsal Attention)	8.20	<0.001
R pSTG (Language)	8.07	<0.001
R ISP (Dorsal Attention)	8.02	<0.001
Superior (Sensorimotor)	7.89	<0.001
L FEF (Dorsal Attention)	7.62	<0.001
L IPS (Dorsal Attention)	7.37	<0.001
R Lateral (Visual)	7.12	<0.001
ACC (Cingulo-opercular)	6.78	<0.001
L pSTG (Language)	6.67	<0.001
L Lateral (Visual)	6.30	<0.001
R IFG (Language)	4.77	0.001
L IFG (Language)	4.72	0.001

For the older adult group, average functional connectivities from left and right Heschl’s gyrus to ROIs within each brain network are characterized in Figures 4 and 5, respectively, and Table 3. In older adults, left Heschl’s gyrus was significantly and positively connected to right Heschl’s gyrus and all ROIs of the sensorimotor, language, cingulo-opercular, dorsal attention, and visual networks (except for the occipital visual network ROI) ($p<0.028$). Left Heschl’s gyrus was also positively connected to the medial prefrontal cortical ROI of the default mode network ($p=0.013$). Similar to the left, right Heschl’s gyrus in older adults was significantly and positively connected to contralateral Heschl’s gyrus and all regions of the sensorimotor and cingulo-opercular networks ($p<0.001$). In addition, right Heschl’s gyrus was positively connected to the medial prefrontal cortical ROI of the default mode network ($p=0.004$). However, right Heschl’s gyrus connectivity differs from the left as it was only connected to the posterior ROIs of the language network ($p<0.001$), only the medial region of the visual network ($p=0.004$), and the left and right frontal eye field regions of the dorsal attention network ($p<0.007$).

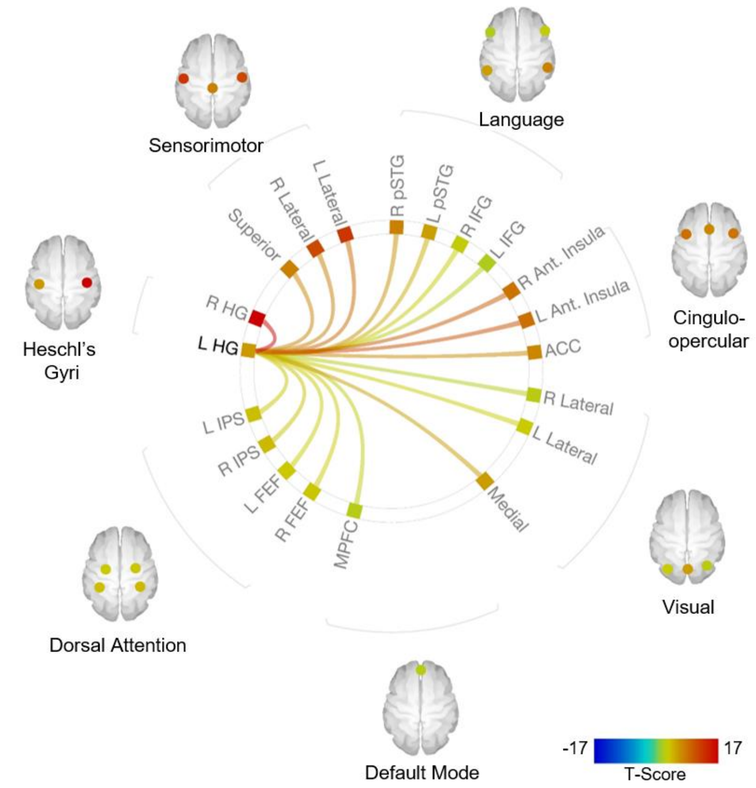

Figure 4. Functional connectivity between left Heschl's gyrus and several brain networks in the older adult group, p<0.05, FDR. Line colors reflect the T-score with warmer colors reflecting larger, positive T-scores.

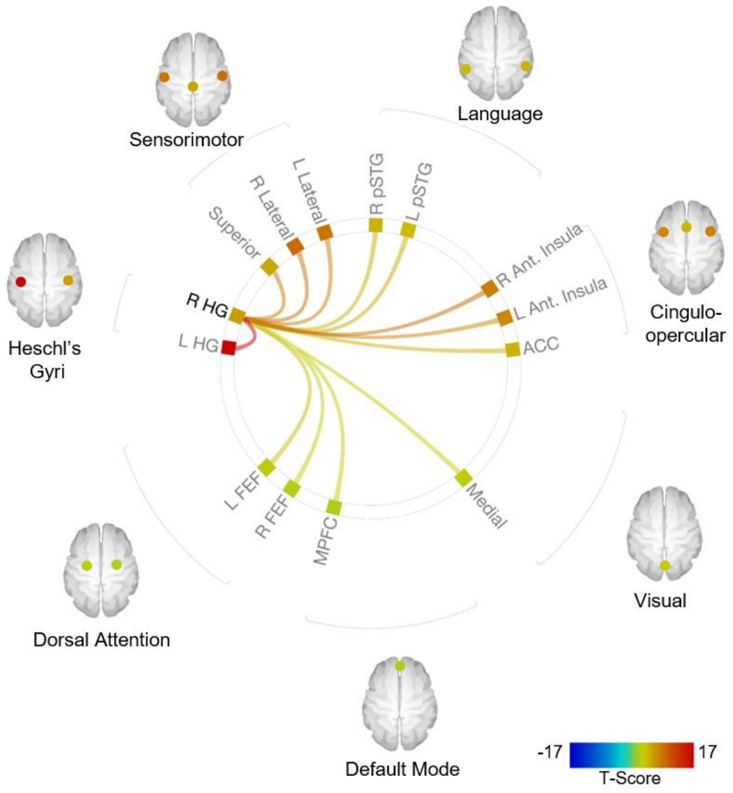

Figure 5. Functional connectivity between right Heschl's gyrus and several brain networks in the older adult group, p<0.05, FDR. Line colors reflect the T-score with warmer colors reflecting larger, positive T-scores.

Table 3. ROI-to-ROI functional connectivity from Heschl's gyrus to network ROIs within older adult group

ROI (Network)	T-value	p value
Left Heschl's Gyrus		
R Heschl's Gyrus	17.77	<0.001
L Anterior Insula (Cingulo-opercular)	11.35	<0.001
R Anterior Insula (Cingulo-opercular)	10.58	<0.001
L Lateral (Sensorimotor)	9.63	<0.001
R Lateral (Sensorimotor)	8.22	<0.001
Superior (Sensorimotor)	7.80	<0.001
ACC (Cingulo-opercular)	7.42	<0.001
R pSTG (Language)	6.99	<0.001
Medial (Visual)	6.23	<0.001
L pSTG (Language)	5.26	<0.001
R IPS (Dorsal Attention)	4.14	<0.001
L IPS (Dorsal Attention)	3.85	0.001
R FEF (Dorsal Attention)	3.64	0.002
L Lateral (Visual)	3.54	0.003
L FEF (Dorsal Attention)	3.52	0.003
R IFG (Language)	3.46	0.003
MPFC (Default Mode)	2.79	0.013
L IFG (Language)	2.57	0.022
R Lateral (Visual)	2.40	0.031

Right Heschl's Gyrus		
L Heschl's Gyrus	17.77	<0.001
R Anterior Insula (Cingulo-opercular)	9.20	<0.001
R Lateral (Sensorimotor)	8.72	<0.001
Superior (Sensorimotor)	8.10	<0.001
L Lateral (Sensorimotor)	8.05	<0.001
L Anterior Insula (Cingulo-opercular)	7.64	<0.001
L pSTG (Language)	5.20	<0.001
R pSTG (Language)	5.06	<0.001
ACC (Cingulo-opercular)	4.94	<0.001
L FEF (Dorsal Attention)	4.34	<0.001
Medial (Visual)	3.43	0.004
MPFC (Default Mode)	3.38	0.004
R FEF (Dorsal Attention)	3.12	0.008

Age group differences in Heschl's gyrus connectivity

Independent samples t-tests between age groups comparing the average ROI-to-ROI connectivity between right and left Heschl's gyri and each network ROI with Bonferroni multiple comparison correction ($p<0.05/22 = 0.002$) revealed significant decreases in connectivity in the older adults compared to the younger adult group (Table 4). Connectivity between left Heschl's gyrus and the bilateral intraparietal sulci and left frontal eye field ROIs of the dorsal attention network were decreased in older adults compared to younger adults ($p<0.001$). Similarly, the medial, left lateral, and right lateral ROIs of the visual network, as well as the superior, left lateral, and right lateral ROIs of the sensorimotor networks were decreased in older adults compared to the younger adults ($p<0.001$). These decreases in Heschl's gyrus connectivity with ROIs of the dorsal attention, visual, and sensorimotor networks in the older versus younger adults were mirrored in right Heschl's gyrus ($p<0.001$). Additionally, older adults exhibited less connectivity between right Heschl's gyrus and the right frontal eye field ROI of the dorsal attention network compared to younger adults ($p<0.001$). The complete results of the independent samples t-test between age groups for all ROIs are provided in the Supplementary Materials.

Table 4. Differences in functional connectivity from left and right Heschl's gyrus to network ROIs between age groups

ROI (Network)	OA mean (sd) connectivity	YA mean (sd) connectivity	T-value	p value
Left Heschl's Gyrus				
L IPS (Dorsal Attention)	0.15 (0.22)	0.42 (0.18)	-5.02	<0.001
R Lateral (Visual)	0.09 (0.21)	0.33 (0.17)	-4.91	<0.001
L Lateral (Visual)	0.12 (0.19)	0.35 (0.18)	-4.81	<0.001
R Lateral (Sensorimotor)	0.43 (0.29)	0.70 (0.22)	-3.99	<0.001

L Lateral (Sensorimotor)	0.49 (0.29)	0.74 (0.21)	-3.82	<0.001
R IPS (Dorsal Attention)	0.17 (0.22)	0.35 (0.15)	-3.81	<0.001
Superior (Sensorimotor)	0.29 (0.21)	0.52 (0.26)	-3.67	<0.001
Medial (Visual)	0.06 (0.18)	0.40 (0.19)	-3.65	<0.001
L FEF (Dorsal Attention)	0.13 (0.21)	0.32 (0.20)	-3.63	<0.001
Right Heschl's Gyrus				
R Lateral (Visual)	-0.002 (0.21)	0.30 (0.22)	-5.62	<0.001
L Lateral (Sensorimotor)	0.32 (0.22)	0.58 (0.27)	-5.48	<0.001
L IPS (Dorsal Attention)	0.06 (0.20)	0.34 (0.25)	-5.02	<0.001
L Lateral (Visual)	0.01 (0.20)	0.27 (0.21)	-4.89	<0.001
Medial (Visual)	0.11 (0.18)	0.34 (0.21)	-4.75	<0.001
R IPS (Dorsal Attention)	0.06 (0.21)	0.33 (0.23)	-4.74	<0.001
R Lateral (Sensorimotor)	0.35 (0.22)	0.69 (0.27)	-4.16	<0.001
Superior (Sensorimotor)	0.20 (0.14)	0.42 (0.29)	-3.74	<0.001
L FEF (Dorsal Attention)	0.11 (0.14)	0.26 (0.18)	-3.73	<0.001
R FEF (Dorsal Attention)	0.09 (0.15)	0.22 (0.14)	-3.58	<0.001

Heschl's gyrus connectivity differences as a function of hearing loss versus age in older adults

To examine the effects of age-related hearing loss on Heschl's gyrus connectivity with each network ROI compared to other effects of age, connectivity was correlated with hearing loss controlling for age, and vice versa, within the older adult group. The analysis correlating hearing loss with connectivity, controlling for age, yielded the following (Figure 6): There were no significant correlations between functional connectivity of left Heschl's gyrus and network ROIs with hearing loss, controlling for age. But from right Heschl's gyrus, hearing loss was correlated with increased connectivity to: the anterior cingulate cortex (p=0.021), right anterior insula (p=0.026), and left anterior insula (p=0.044) ROIs of the cingulo-opercular network, as well as the right inferior frontal gyrus ROI of the language network (p=0.026). None of the correlations of connectivity with age, controlling for hearing loss (p<0.05, FDR corrected) were significant.

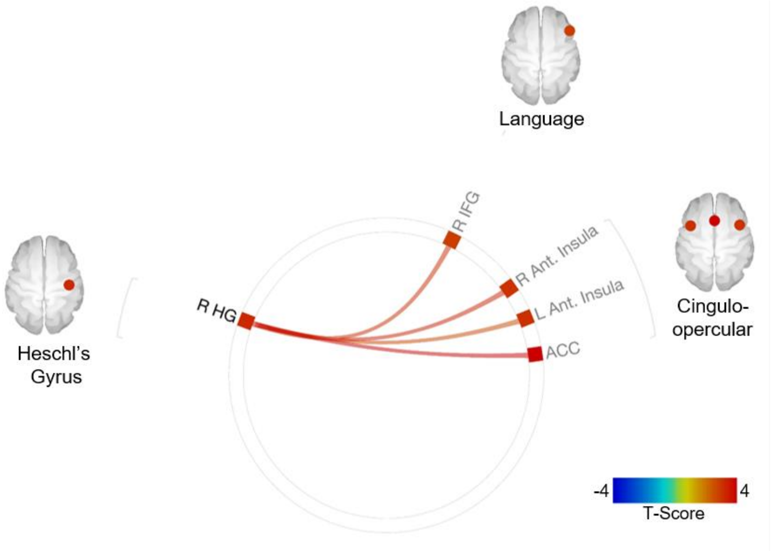

Figure 6. Correlation between participant hearing loss and functional connectivity between right Heschl's gyrus and brain networks, controlling for participant age, $p<0.05$, FDR. Line colors reflect the T-score with warmer colors reflecting larger, positive T-scores.

Discussion

The aim of the present study was to characterize the functional connectivity of Heschl's gyrus with well-characterized cognitive and sensorimotor networks, and to characterize how this connectivity varies with age and specifically with age-related hearing loss. The impact of hearing loss upon the brain in older adults, and how it differs from the well-studied impact of age more generally, is largely unknown. These findings demonstrate that bilateral Heschl's gyri are functionally connected to intrinsic cognitive and sensorimotor networks in both younger and older adults. However, older adults exhibit reduced connectivity between left and right Heschl's gyri and the dorsal attention, visual, and sensorimotor brain networks compared to younger adults. Within the older adult group, there were no differences in connectivity related to participant age once hearing loss was controlled for, but age-related hearing loss was associated with increased connectivity from right Heschl's gyrus to the cingulo-opercular network and the right inferior frontal ROI of the language network. These findings characterize the extensive functional connectivity of Heschl's gyrus in younger and older adults with cognitive and sensorimotor networks and point to possible neural changes that may serve as compensatory mechanisms in response to age-related hearing loss.

Functional connectivity of Heschl’s gyrus in young adults

The functional connectivity of left and right Heschl’s gyrus to ROIs within well-defined cognitive and sensorimotor brain networks was characterized in a group of younger adults from the HCP. Left and right Heschl’s gyrus were significantly functionally connected to the same regions within the dorsal attention, language, cingulo-opercular, sensorimotor, and visual networks, and to each other. However, the patterns of the strengths of connectivities differed between left and right Heschl’s gyrus. Right Heschl’s gyrus expressed the strongest functional connectivity to left Heschl’s gyrus, followed by ROIs within the sensorimotor network and the cingulo-opercular network. The next strongest connectivities to right Heschl’s gyrus were a mixture of ROIs in the dorsal attention, visual, and language networks. Left Heschl’s gyrus, like the right Heschl’s gyrus, was most significantly connected to the sensorimotor network, followed by right Heschl’s gyrus. However, the similarities to the connectivity pattern of right and left Heschl’s gyrus end there; the remainder of left Heschl’s gyrus’ significant functional connectivities reflected a more distributed pattern of connectivity across the remaining network ROIs, with the strongest connections between left Heschl’s gyrus and the more posterior ROIs of each network, followed by the more anterior ROIs of each network. Also, left (but not right) Heschl’s gyrus was positively functionally connected to the posterior ROIs of the default mode network.

Aside from the strong functional connectivity between left and right Heschl’s gyrus, both left and right Heschl’s gyri were most strongly connected to the left and right lateral ROIs of the sensorimotor network, which encompass the lateral and inferior portions of the precentral and postcentral gyri, and were also strongly connected to the superior ROI of the sensorimotor network (covering the most superior aspects and the medial surface of the precentral and post central gyri). This finding illustrates that bilateral primary auditory cortex is highly functionally connected to primary sensorimotor cortex, aligning with prominent models of auditory processing and auditory-motor integration (Hickok & Poeppel, 2007; Rauschecker & Scott, 2009; Wilson, Saygin, Sereno, & Iacoboni, 2004) Such models typically include dual streams that emanate from Heschl’s gyrus, including a ventral pathway extending anteriorly along the superior temporal gyrus (STG), and a dorsal pathway that generally extends posteriorly along STG and superiorly and anteriorly into premotor and inferior frontal cortex (Alain, Arnott, Hevenor, Graham, & Grady, 2001; Kaas & Hackett, 1999; Rauschecker & Scott, 2009; Rauschecker & Tian, 2000). The dorsal pathway is thought to be involved in auditory-motor integration critical for mapping speech sounds onto articulatory representations for speech production (Hickok & Poeppel, 2007; Rauschecker & Scott, 2009). These results provide further evidence that supports a functional link in humans between Heschl’s gyri and motor cortex within the dorsal auditory processing stream.

The findings reported in this study also reveal that bilateral Heschl’s gyri were highly functionally connected to ROIs within the cingulo-opercular network, particularly bilateral anterior insula to right Heschl’s gyrus. Functional connectivity of Heschl’s gyrus to ROIs within the cingulo-opercular network may offer insight into a mechanism that supports auditory attention processes. Previous work suggests that the cingulo-opercular network is involved in goal-driven behaviors through the initiation and top-down maintenance of task sets, adjusting performance in response to errors to optimize performance (Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008; Dosenbach et al., 2006). The anterior cingulate cortex (ACC) region of this network has been shown to reliably activate following stimuli or response conflict (i.e. as seen in the widely-used color-word Stroop task) in response to both auditory-only and visual-only conflict, but not audiovisual conflict (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Fitzhugh et al., 2019; Milham et al., 2001; Roberts & Hall, 2008). Similarly, others propose that the ACC, as well as bilateral insulae, are involved in top-down control of focal attention (i.e. target detection and awareness), overlapping with the “executive” attention network (Petersen & Posner, 2012). Using the same attention network model put forth by Peterson and Posner (2012), the significant functional connectivity between Heschl’s gyri and the inferior parietal sulcus (IPS) and frontal eye field (FEF) ROIs of the dorsal attention network (predominately investigated in other studies using visual stimuli) implicate a potential mechanism for orienting to external stimuli in the auditory realm. Alternatively, the connection between Heschl’s gyrus and the dorsal attention network, as well as ROIs within the visual network, may point to the neural mechanisms underlying crossmodal attention and visual capture effects (Koelewijn, Bronkhorst, & Theeuwes, 2009).

Decreased Heschl's gyrus functional connectivity in older adults

Functional connectivity from Heschl's gyrus in the younger adult group was strongest with the sensorimotor network, followed by the cingulo-opercular network. However, this pattern is generally reversed in the older adult group: left Heschl's gyrus, was most strongly connected to bilateral insulae of the cingulo-opercular network (and right Heschl's gyrus with right anterior insula), followed by the ROIs of the sensorimotor network. As described above, the cingulo-opercular network is involved in top-down control of attention and conflict monitoring, suggesting that older adults may rely upon attention-mediated resources to a greater degree than younger adults when processing acoustic information. Previous research demonstrates that activation within regions of the cingulo-opercular network is increased in response to acoustic degradation of speech stimuli, when additional attentional resources are required to maximize speech comprehension performance (Peelle, 2018). Both younger and older adults with normal hearing demonstrate increased activation in the cingulo-opercular network in response to degraded speech stimuli, with activation modulated by the level of attention paid to the degraded speech signal (Eckert, Walczak, et al., 2008; Wild et al., 2012). It is likely that older adults have increased attentional demands even while listening to clear speech, as they exhibit elevated levels of activation within the ACC regardless of the level of acoustic clarity (Erb & Obleser, 2013). The adaptability of cingulo-opercular network activity may enhance speech comprehension in older adults: increased activity within the cingulo-opercular network during a speech-in-noise recognition task was found to predict the likelihood of accurate word recognition on the next trial (Vaden et al., 2015). The results of this study nicely complement these task-based fMRI findings. The task-based fMRI findings suggest that older adults may rely upon the cingulo-opercular network to a greater degree than younger adults in response to acoustic challenge to improve comprehension, and these resting-state fMRI results indicate that this cingulo-opercular dependence may relatively strengthen the functional connectivity between the cingulo-opercular network and Heschl's gyrus.

The statistical comparison of the average functional connectivity between age groups reveals that older adults exhibit reduced connectivity from both left and right Heschl's gyri to all ROIs of the sensorimotor network, the bilateral IPS and left FEF in the dorsal attention network, and the medial, left lateral, and right lateral ROIs of the visual network compared to younger adults. At the whole network level, previous studies have shown age-related declines in connectivity within the default mode, motor, dorsal attention, and salience networks (Allen et al., 2011; Andrews-Hanna et al., 2007; Damoiseaux et al., 2008; Onoda et al., 2012; Tomasi & Volkow, 2012), but the findings in this study are, to my knowledge, the first to provide evidence for age-related decreases in functional connectivity between primary auditory cortex (i.e. Heschl's gyrus) and specific regions within other sensory networks.

The older adults' decreases in functional connectivity between Heschl's gyrus and regions of the sensorimotor network compared to younger adults may provide insight into age-related changes within the dorsal language processing stream and its involvement in formulating motor or articulatory representations of auditory stimuli (Hickok, Buchsbaum, Humphries, & Muftuler, 2003; Warren, Wise, & Warren, 2005). Older adults are more likely to make speech production errors known as slips of the tongue (e.g. saying "coffee *cot*" instead of "coffee *pot*") and are more likely to make omission errors during slips of the tongue (MacKay & James, 2004). Word finding and retrieval problems are also common among older adults (L. E. James & Burke, 2000). Such errors are not thought to result from deficits in word meaning, as semantic knowledge remains stable with age, but instead reflect insufficient activation of phonological representations necessary for production (Burke & Shafto, 2008). It is possible that such observed declines in speech production in older adults may result from decreases in connectivity within the dorsal processing stream of language, including between Heschl's gyrus and the sensorimotor cortex.

Regarding speech perception, the ability to integrate visual information from the speaker (e.g. articulatory movements and facial expressions) greatly improves comprehension of the auditory signal (Summerfield, 1992). Older adults typically do not demonstrate age-related declines in audio-visual integration compared to younger adults, particularly once differences in individual auditory and visual acuity are controlled, and may even show enhanced integration compared to younger adults (Cienkowski & Carney, 2002; Laurienti, Burdette, Maldjian, & Wallace, 2006; Sommers, Tye-Murray, & Spehar, 2005). The reported findings of reduced functional connectivity between right Heschl's gyrus and regions within the visual and dorsal attention network in older adults seem contradictory to age-related audiovisual facilitation effects. However, previous research has shown that the temporal window within which two multisensory stimuli must occur in order to integrate becomes longer with age, likely to compensate for declines in sensory acuity with age, making the integration process more susceptible to distraction (Diederich, Colonius, & Schomburg, 2008). Thus, while audiovisual integration may be enhanced in some ways in older adults, decreased functional connectivity between auditory and visual processing areas in older adults may be related to longer time needed for integration.

Hearing loss increases Heschl's gyrus functional connectivity

This study revealed that age-related hearing loss was positively correlated with functional connectivity from right Heschl's gyrus to the cingulo-opercular network and a region of the language network in older adults. In other words, as the level of hearing loss increased so too did the functional connectivity between right Heschl's gyrus and these two networks. Critically, there were no differences in functional connectivity from Heschl's gyri associated with age within the older adult group, suggesting that the findings reported here more likely reflect changes with hearing loss and not other age-related declines. Furthermore, the alterations in connectivity with age-related hearing loss within the older adult group are distinct from the differences in connectivity observed between the young and older adult groups. These differences are consistent with the idea that this work has identified alterations in functional connectivity associated with age-related hearing loss, independent from the effects of age.

In comparison, the small body of previous literature using resting-state fMRI to explore the impact of age-related hearing loss on functional connectivity only report effects between

Heschl's gyrus and the visual MT+ area, as well as within the dorsal attention and default mode networks (Husain et al., 2014; Puschmann & Thiel, 2017; Schmidt et al., 2013). However, differences in methodological approach and participant groups may explain the discrepancies between these previous studies and the findings reported here. In the study by Husain et al. (2014), while they similarly used ROIs within left and right Heschl's gyrus, their approach differed from this experiment in two ways: 1) they treated the Heschl's gyri ROIs as a pair and averaged connectivity across the pair and 2) they assessed connectivity from the average of Heschl's gyri to all other voxels of the brain. This study measured connectivity from left and right Heschl's gyrus independently and it reduced the number of comparisons by assessing connectivity to a set of ROIs. It is likely that these differences in methodologies increased the statistical power in this study, allowing the effect that hearing loss has upon connectivity of Heschl's gyrus to other cortical networks to be observed. The study by Puschmann and Thiel (2017) reported increased functional connectivity between left Heschl's gyrus and visual area MT+ with increasing hearing loss in a group of older adults. The data in this study only show differences in functional connectivity between right Heschl's gyrus and the right lateral ROI of the visual network (a right homologous region in close proximity to Puschmann and Thiel's reported visual area MT+) in the comparisons of younger and older adults, not with age-related hearing loss within the older adult group. However, these authors also measured connectivity across both left and right Heschl's gyri together, again suggesting that the functional connectivity of left and right Heschl's gyrus should be evaluated separately.

While differences in methodologies may explain the discrepancies between these findings and those of the few studies that previously have explored resting-state functional connectivity differences associated with age-related hearing loss, the results of this experiment align well with task-based fMRI findings of age-related hearing loss. This study illustrates that age-related hearing loss is associated with functional connectivity increases between primary auditory cortex and the cingulo-opercular network. One task-based fMRI study shows that hearing loss is associated with greater activation for clear speech than acoustically degraded speech in the right anterior insula (part of the cingulo-opercular network), even after controlling for age (Erb & Obleser, 2013). This pattern is typically observed in younger adults and older adults with better hearing abilities for more acoustically challenging (i.e. degraded) speech conditions (Adank, 2012; Erb, Henry, Eisner, & Obleser, 2013; Erb & Obleser, 2013; Vaden et al., 2015). This suggests that older adults with a hearing loss must recruit attentional cognitive resources supported by the cingulo-opercular network even in clear listening conditions, increasing their listening effort. The prolonged coupling of auditory and attention-related network activation that occurs throughout the gradual onset of age-related hearing loss may result in increased functional connectivity between Heschl's gyrus and regions of the cingulo-opercular network as observed in this study.

Lastly, this study reported increased functional connectivity with age-related hearing loss between right Heschl's gyrus and the right inferior frontal gyrus (IFG) of the language network. While the left IFG (i.e. Broca's area) is frequently implicated in studies of language production, it also is posited to be involved in domain-general aspects of language comprehension, such as cognitive control and working memory (Hagoort, 2005; LaCroix, Diaz, & Rogalsky, 2015; Rogalsky & Hickok, 2011; Rogalsky, Matchin, & Hickok, 2008), although its exact roles are still debated (Fedorenko, Behr, & Kanwisher, 2011; Rogalsky & Hickok, 2011). The right IFG is not included in most prominent language processing models (Binder et al., 2000; Friederici, 2012; Hickok & Poeppel, 2007; Rauschecker & Scott, 2009; Lorraine K Tyler & Marslen-Wilson, 2008). However, it has been identified in studies using functional connectivity to define language processing networks because it does exhibit strong functional connectivity with left IFG and bilateral posterior superior temporal regions (Saur et al., 2010; Tomasi & Volkow, 2012; Turken & Dronkers, 2011), which are mainstays in functional neuroanatomical models of language. Right IFG involvement during language processing has previously been observed in individuals with left hemispheric, aphasic stroke, however, it is unclear if this recruitment of the right hemisphere homologue of Broca's area actually improves language comprehension (Anglade, Thiel, & Ansaldo, 2014; Geranmayeh, Brownsett, & Wise, 2014; Richter, Miltner, & Straube, 2008).

The respective roles of left and right IFG recruitment in older adults in response to speech stimuli also are unclear. Studies have shown that as speech stimuli becomes more phonologically or syntactically complex, older adults exhibit reduced activation in left inferior frontal regions relative to younger participants (Peelle et al., 2009; Shafto, Randall, Stamatakis, Wright, & Tyler, 2012) and additional activation in right IFG, possibly supporting syntactic processing of the left IFG (Tyler et al., 2009). While other studies using visually-presented sentences found increased activation in dorsal regions of the left inferior frontal gyrus in older compared to younger adults, with similar behavioral performance between groups, and suggest that this activation may represent the recruitment of working memory resources (Fitzhugh, Braden, Sabbagh, Rogalsky, & Baxter, In Press; Grossman et al., 2002; Wingfield & Grossman, 2006). Thus, while these findings are the first to link alterations in right IFG connectivity with age-related hearing loss, based on previous literature of the IFG's role in language comprehension in older adults, it is possible that the increases in functional connectivity reported here reflect enhanced recruitment of domain-general resources that support language processing (e.g. cognitive control or working memory) with hearing loss.

While overall the older adult group expressed an evenly distributed range of hearing abilities, as shown in Figure 1, the levels of hearing ability only ranged from normal hearing to a moderate hearing loss. Future studies should include more individuals with moderate to severe levels of hearing loss to more fully characterize the impact of hearing loss on brain functional connectivity. Including groups of younger to middle-aged adults with a range of hearing abilities will also reveal if these functional connectivity differences reflect alterations with age-related hearing loss specifically, or instead reflect adaptations in response to hearing loss, regardless of age. The potential influences of hearing aid usage, on functional connectivity also should be investigated. In this study, four individuals reported wearing hearing aids. Currently, it is unclear if the use of hearing aids may lead to differences in functional connectivity compared to those with a hearing loss who do not wear hearing aids. If so, functional connectivity may serve as an indicator of the efficacy of hearing corrective technologies, possibly serving as a useful tool in studies that investigate age-related hearing loss as a modifiable target of cognitive decline.

Conclusion

In the present study, resting-state fMRI was used to investigate differences in the functional connectivity of Heschl’s gyrus between young and older age groups and with age-related hearing loss in the group of older adults. Functional connectivity in the younger adult group revealed that left and right Heschl’s gyri are positively connected to many brain networks including the dorsal attention, language, cingulo-opercular, sensorimotor networks, and portions of the visual and default mode networks. Older adults expressed a similar pattern of functional connectivity between Heschl’s gyri and the brain networks of interest. Tests of age differences in functional connectivity between the age groups reveal that older adults have significantly lower functional connectivity between Heschl’s gyrus and regions of the sensorimotor, dorsal attention, and visual networks. However, these age differences are distinct from connectivity differences associated with age-related hearing loss. Within the older adult group, these data reveal that, after controlling for age, age-related hearing loss is associated with increased functional connectivity between right Heschl’s gyrus and regions of the cingulo-opercular network and the right inferior frontal gyrus of the language network. There were no differences in connectivity with age, controlling for hearing levels, within the older adult group. Together these findings indicate that there are unique age and age-related hearing loss differences in Heschl’s gyrus functional connectivity with brain networks.

CHAPTER 3

EXPERIMENT 2: BEHAVIORAL AND NEURAL NETWORK MEASURES OF WORKING MEMORY AND ATTENTIONAL CONTROL AND THEIR CONTRIBUTIONS TO AUDITORY SPEECH COMPREHENSION IN OLDER ADULTS

Introduction

Approximately one-third of older adults struggle with understanding everyday conversations, particularly ones that include complex sentence structures (e.g. sentences that deviate from the typical subject-verb-object order in English, such as those with embedded clauses) or that occur in noisy environments (Committee on Hearing, Bioacoustics, and Biomechanics, 1988; Hamilton-Wentworth District Health Council, 1988; Helfer, Merchant, & Wasiuk, 2017; Humes, 1996). However, it is unclear if these communication difficulties are solely explained by age-related hearing loss or if they can also be contributed to older adults' individual cognitive abilities. As many as 15% of adults aged 50 in the United States have at least a mild hearing loss within speech-sound frequencies (i.e. 500 – 4000 Hz), with this rate doubling every 10 years; while an even greater proportion of older adults experience hearing loss within higher frequencies (>4000 Hz) (Agrawal et al., 2008; Lin, Thorpe, et al., 2011). Despite this, a majority of older adults with a hearing loss do not wear corrective devices like hearing aids, the most common treatment for managing age-related hearing loss (Chien & Lin, 2012; Lin, Thorpe, et al., 2011).

While hearing loss is a prominent contributor to deficits in communication (Pichora-Fuller & Souza, 2003; Schneider, Daneman, & Murphy, 2005; Schneider et al., 2002), studies that restore audibility via acoustic manipulations similar to those employed by hearing aids reveal that cognitive factors also significantly contribute to older adults' ability to understand both speech in quiet and in noise (Humes, 2007). Several other studies have reported a similar relationship between auditory speech comprehension and cognition (for a review see Akeroyd, 2008) even in older adults with normal hearing levels (Besser, Festen, Goverts, Kramer, & Pichora-Fuller, 2015; Desjardins & Doherty, 2013; Fullgrabe, Moore, & Stone, 2015). Thus, once controlling for hearing loss, it is likely that cognitive abilities also contribute to auditory speech comprehension in older adults, particularly for language with complex sentence structures and speech that occurs in noisy environments.

Previous studies that have explored the relationship between cognitive resources and comprehension of complex sentence structures identify working memory as a significant contributor to comprehension abilities, such that better sentence comprehension is associated with better working memory spans (Caplan & Waters, 1999; Evans et al., 2015; Just & Carpenter, 1992), particularly in older adults (DeDe, Caplan, Kemtes, & Waters, 2004; Goral et al., 2011; Kemper & Liu, 2007; Norman et al., 1992). However, there is much debate as to the exact mechanisms of working memory during language comprehension (Caplan & Waters, 2013, 1999; Just & Carpenter, 1992; McElree, Foraker, & Dyer, 2003).

Regarding language comprehension in noisy or degraded situations, the Ease of Language Understanding model (ELU; Rönnberg, Rudner, Foo, & Lunner, 2008) offers a framework for describing the role which cognitive resources play in auditory speech comprehension in older adults. This model proposes that when an incoming speech signal does not match with known phonological representations (as is likely to occur with hearing loss or in noisy environments), working memory processes are required to resolve the mismatch between the perceived signal and known representations of syllables and words (Rönnberg et al., 2008). This model was extended to include aspects of attentional control, specifically inhibition, that are involved in selecting the correct signal from competing target speech signals and other background speakers or noise (Rönnberg et al., 2013). This addition is in line with several other studies which attribute successful comprehension of sentences in multi-speaker backgrounds to attentional control in older adults (Anderson, White-Schwoch, Parbery-Clark, & Kraus, 2013; Janse, 2012; Meister et al., 2013), while others also attribute it to working memory (Desjardins & Doherty, 2013; Fullgrabe et al., 2015; P. J. James, Krishnan, & Aydelott, 2014; Ward, Rogers, Van Engen, & Peelle, 2016; Zekveld, Rudner, Johnsrude, & Rönnberg, 2013).

FMRI has been extensively used in younger adults to characterize the brain regions involved in speech comprehension, identifying the bilateral superior and middle temporal gyri and inferior parietal lobes, and left inferior frontal gyrus (i.e. Broca’s area) as major hubs involved in comprehension (Binder et al., 2000; Friederici, 2012; Hickok & Poeppel, 2007; Rauschecker & Scott, 2009; Tyler & Marslen-Wilson, 2008). Studies of the neurobiological processes involved in processing complex sentence structure in older adults compared to younger adults reveal that older adults exhibit reduced brain activation in left inferior frontal gyrus but increased activation in right inferior frontal gyrus, middle and superior frontal cortex, bilateral precentral gyrus and parietal cortex (near the intraparietal sulcus) (Peelle, Troiani, Wingfield, & Grossman, 2009; Tyler et al., 2009). These regions fall outside of the typical language processing system but overlap with regions of a frontoparietal network encompassing left and right lateral prefrontal cortex and the intraparietal sulcus and the surrounding cortex (Marek & Dosenbach, 2018). Yet there is conflicting evidence to suggest if these differences in activation observed in the older adults result in improved language comprehension (Grossman et al., 2002; Peelle et al., 2009).

Other studies have investigated the cognitive and neural resources involved in processing speech in noisy environments by applying energetic or informational masking (i.e. typically broadband noise or multi-speakers, respectively) over the target stimuli or by degrading the quality of the target stimuli via noise vocoding. Comprehension of speech in informational masking is reduced compared to speech in energetic masking in older adults and is posited to increase cognitive load, relying upon working memory and attentional control abilities to a greater degree (Helfer et al., 2017; Peelle, 2018; Rajan & Cainer, 2008; Schneider, Li, & Daneman, 2007). Increased activation within a cingulo-opercular network (i.e. anterior cingulate and bilateral insulae; Dosenbach et al., 2007) is often observed in response to acoustically degraded speech stimuli compared to clear speech, in both younger and older adults (Adank, 2012; Eckert, Walczak, et al., 2008; Erb et al., 2013; Erb & Obleser, 2013; Vaden et al., 2013). Activation in these regions has also been shown to predict accurate comprehension of degraded speech for single words (Vaden et al., 2015; Wild et al., 2012). Other studies have found increased activation for acoustically degraded speech (single words and sentences) in right frontal cortex, including right middle frontal and precentral gyri, and right posterior parietal cortex, in both younger and older adults (Lee, Min, Wingfield, Grossman, & Peelle, 2016; Wong et al., 2009).

Collectively, investigations into the neural mechanisms through which older adults process sentences with complex structure and speech in difficult listening environments (e.g. speech in informational masking) both implicate working memory and attentional control resources supported by frontoparietal and cingulo-opercular brain networks (Dosenbach et al., 2007; Elton & Gao, 2014; Marek & Dosenbach, 2018; Niendam et al., 2012; Owen, McMillan, Laird, & Bullmore, 2005; Petersen & Posner, 2012). However, effects of complex sentence structures and difficult listening environments previously have not been studied within the same participants, let alone within the same experimental paradigm using both behavioral and fMRI measures. Thus, it is unclear if these two types of difficult speech comprehension, and the common combination of the two, are using distinct or shared cognitive resources.

In this study, resting-state fMRI and behavioral measures were used to investigate how working memory and attentional control may contribute to comprehension of structurally and acoustically complex speech in cognitively normal older adults. Resting-state fMRI was used as it is a powerful tool to investigate brain networks in the absence of any task, avoiding introducing task- or stimuli-related confounds, while still capturing the brain networks that are modulated during cognitive tasks (Calhoun et al., 2008; S. M. Smith et al., 2009). Critically, unlike most previous work, this study aimed to specifically examine the brain networks associated with both working memory and attentional control (that are often implicated in language comprehension tasks) without task-related confounds, within the same participants, and while controlling for hearing loss. This study investigated these brain networks using measures of functional connectivity (i.e. correlations between intrinsic activation patterns of anatomically distinct brain regions) which are thought to reflect the relative integrity of functional communication between or within the networks (van den Heuvel & Hulshoff Pol, 2010). It was predicted that better scores on behavioral measures of working memory and increased functional connectivity of the frontoparietal network would be associated with better comprehension abilities of complex sentence structures. It was further predicted that better scores on behavioral measures of attentional control and increased functional connectivity of the cingulo-opercular network would be associated with better comprehension abilities of speech in informational masking. Lastly, better comprehension abilities for sentences with the combination of complex structure and informational masking will be associated with both better working memory and attentional control measures.

Methods

Participants

The 31 older adults from Experiment 1 also participated in the present study. Participants were aged 60 to 80 years (20 women; mean(sd) age = 67.77(5.63) years, mean(sd) education = 17.53(3.32) years) and met the same inclusion criteria as in Experiment 1. Pure-tone audiometry was used to determine participant hearing ability (i.e. pure-tone average, PTA) using the procedure described in Experiment 1, where a higher average threshold indicates greater hearing loss (mean(sd) = 26.76(12.01) dB, range = 6.25 – 52.92 dB; see Experiment 1, Figure 1). Hearing ability did not significantly correlate with participant age (r =0.320, p=0.080). Visual acuity was evaluated, with corrective lenses if typically worn or required for reading, using a standard Snellen eye chart and Ishihara's Color Plates (Ishihara, 1969) to ensure participants could identify written and color stimuli. All participants exhibited 20/30 vision or better and reported mean±sd = 14.66±0.72 correct out of 15 color-vision plates, where >13 is considered normal (Ishihara, 1969). Written informed consent was obtained from each participant in accordance with Arizona State University's Institutional Review Board guidelines. Participants were compensated monetarily for their efforts.

Language and cognition assessments

Language: A sentence-picture matching task, adapted from Wilson et al. (2010) was used to evaluate auditory speech comprehension. In this task, participants were auditorily presented with a sentence and visually presented simultaneously with a picture pair. Participants were instructed to select the picture that matches the sentence as quickly and accurately as possible.

Target sentences were created by Wilson et al. (2010) and contained two high-frequency nouns (boy and girl), one of seven high-frequency verbs (e.g. push, pull, kiss), and one of three high-frequency color adjectives (blue, red, green) to minimize lexical demands. Sentences were digitally recorded by a single, classically trained, male vocalist with a standard American English accent, lowpass filtered, and denoised. The sentences were presented in one of six conditions: two levels of sentence structure (canonical and noncanonical) and three levels of background noise (multi-speakers, broadband, and silence). The multi-speakers and broadband levels of background noise represented informational and energetic masking, respectively. The multi-speaker background was derived from overlaying onto a single track four speakers (two male and two female) which were reading aloud sentences from the AzBio test corpus (Spahr et al., 2012). A single sample of the multi-speakers recording was selected and applied as background noise to all target sentences. The broadband background noise was created by generating a filter shaped to the long-term average spectrum of the multi-speakers' sample and applying this filter to a sample of white noise.

Background noise samples were added to each sentence recording and started 500ms prior to the onset of the sentence and extended 500ms beyond the offset of the sentence. The signal-to-noise ratio of the sentence to background noise was set to +2dB, slightly enhancing the audibility of the sentence recording. All audio recordings were modified and combined using Audacity® 2.2.1 (https://audacityteam.org/). The mean±sd sentence duration was 2.78±0.12 seconds and did not differ between sentence structure type (canonical mean±sd 2.77±0.13 s and noncanonical mean±sd 2.79±0.11 s, t(34)=0.02, p=0.51).

In total, 60 sentences were generated with 10 unique sentences in each of the six task conditions. Sentences were evenly divided into two blocks with five sentences per condition (30 total sentences per block) and five null trials (only a fixation cross on the screen and no auditory stimuli) per block, all randomly presented without replacement. Each trial began with a fixation cross for 1000ms followed by the simultaneous presentation of the auditory and visual stimuli. Auditory sentences were only presented once. The presented picture pair consisted of a target picture that matched the sentence and a foil that either represented a different action verb or a reversal of agent and patient. The pictures remained on the screen until a response was made via button press. Upon selection, trials ended with a 1000ms fixation cross. Participants were provided with verbal and written instructions and practice trials with all sentence structures and background noise. Participants could repeat the practice if requested. The duration of each block was approximately five minutes, depending on the response time of the participant.

Each response was scored for accuracy and reaction time (RT). To compute average RT, only correct responses were included and RTs greater than 2.5 standard deviations from the overall mean reaction time for each participant were discarded (mean = 1.6% trials discarded per participant) (Baayen & Milin, 2010; Lachaud & Renaud, 2011; Ratcliff, 1993). Accuracy, mean RT, and RT difference scores computed between task conditions of interest (see *Statistical Analysis* section below for computation) were used as dependent variables in statistical analyses.

Cognition: Measures of working memory and attentional control were collected as part of a larger battery of neuropsychological assessments and experimental tasks. E-Prime Standard 2.0 software (Psychology Software Tools, Pittsburgh, PA) was used on a Dell Precision PC laptop to program and deliver all computerized experimental tasks, recording reaction time and/or accuracy, depending on the task. See Appendix A, Table A1 for participant mean(sd) performance for all tasks in the test battery.

A modified version of the Operation Span Task (OST) was used as a measure of complex verbal working memory and administered via computer (Foster et al., 2015; Oswald, McAbee, Redick, & Hambrick, 2015). Briefly, following a practice procedure, participants performed two tasks simultaneously: a) a distractor task where they were to determine the accuracy of an arithmetic problem (e.g. “(6/3)+1=3?”) via mouse click (“True” or “False”); and b) a target task of remembering and later recalling a single consonant letter (e.g. “H”) briefly presented on the screen. The experimental procedure alternated between distractor and target trials for a given set size of distractor and target trial pairs. At the end of each set, participants were asked to recall the letters presented in the order they were presented. However, final scoring disregarded recall order; instead, one point was given for each correctly recalled letter regardless of order, as previous studies indicate this metric has better psychometric properties (e.g. more reliable and sensitive to individual differences in working memory) (Conway et al., 2005; Redick et al., 2012). The OST had a maximal score of 21.

Since the use of the OST has not previously been published in an older adult population, the following modifications were made from the original protocol described in Oswald and colleagues (2015) to mitigate fatigue: 1) set size range was reduced from four to six distractor-target pairs to two to five pairs, with two administrations of set sizes three and four; 2) set sizes were modified to present in sequential order, as opposed to randomly; 3) the delay after the target stimuli was increased from 250ms to 1000ms; 4) the arithmetic operations were simplified; and 5) participants were given the option to verbally respond to arithmetic and letter recall if they felt uncomfortable with using a computer mouse; the task administrator operated the mouse following participant responses.

The Simon Task was used to assess attentional control (Castel, Balota, Hutchison, Logan, & Yap, 2007). In this computerized task, an arrow appeared on the screen, pointing to either the left or the right, and participants were instructed to indicate via button press the direction in which the arrow was pointing (e.g. if the arrow pointed to the right, press the right button). Arrows could appear in one of three places on the screen along the same central, horizontal axis: the left third, right third, or middle of the screen. With this paradigm, trials could be congruent, wherein the arrow direction matched the arrow placement (e.g. a left-pointing arrow appearing in the left third of the screen); incongruent, wherein the arrow direction and arrow placement were conflicting (e.g. a left-pointing arrow appearing in the right third of the screen); or neutral, wherein the arrow is positioned in the middle of the screen pointing in either direction. Experimental trials included 40 congruent, 40 incongruent, and 40 neutral trials randomly presented without replacement. Trials were evenly divided between two blocks, each approximately 5 minutes in duration. Accuracy and RT were recorded for each trial. To compute average RT, only correct responses were included and RTs greater than 2.5 standard deviations from the overall mean reaction time for each participant were discarded (mean = incongruent: 4.3%, congruent: 1.8%, neutral: 1.7% trials discarded per participant). An RT difference score between incongruent and neutral trials was computed as the independent measure of attentional control from this task.

Subtests of the Wechsler Adult Intelligence Scale 4th edition (WAIS-IV) were administered to collect covariate measures of interest (Wechsler, Coalson, & Raiford, 2008). The Digit Span (Forward, Backward, and Sequencing) and the Arithmetic subtests comprise the Working Memory Index (WMI), which was used as a measure of simple working memory. The Symbol Search and Coding subtests comprise the Processing Speed Index (PSI), which was used as a measure of speed of processing.

MRI acquisition and analysis

Scanning was conducted at the Barrow Neurological Institute in Phoenix, AZ on a research-dedicated 3T Phillips Ingenia scanner. As in Experiment 1, resting-state fMRI data were collected using single-shot EPI pulse sequences with ADNI 3 imaging parameters (Weiner et al., 2017) and were as follows: one 10-minute run, TR=3000ms, TE=30ms, flip angle=90°, FOV=217 x 217, matrix=64 x 62, 48 axial slices, 3.39mm slice thickness, in-plane resolution=3.39x3.39mm. Fieldmaps were also collected to correct for field inhomogeneity using the following parameters: TR=20ms, TE (short)=2.3ms, TE (long)=4.6ms, flip angle=10°, FOV=240 x 240, matrix=80x80, voxel size=3 x 3 x 3mm, 52 sagittal slices, acquisition time =1 minute 22 seconds. T1 anatomical scan was also acquired for each participant. The imaging parameters were as follows: MPRAGE sequence, TR=6.74s, TE=3.10ms, flip angle=9°, FOV=270 x 253, matrix=256x256, voxel size=1.1 x .1.1 x 1.2mm, 170 sagittal slices, acquisition time =5 minutes 34 seconds.

MRIcron (Rorden & Brett, 2000) was used to reconstruct the resting-state functional images. Pre-processing and analysis of the resting-state functional neuroimaging data was performed using Functional Connectivity Toolbox (CONN; Whitfield-Gabrieli & Nieto-Castanon, 2012). This program calls upon SPM12 functions to conduct the following pre-processing procedures on the functional images: slice-timing correction, realignment, coregistration to each participant’s anatomical scan, normalization to the MNI template, and spatial smoothing with an 8mm FWHM Gaussian kernel. Fieldmaps were created using SPM12’s FieldMap toolbox and applied to CONN's pre-processing pipeline to correct for field inhomogeneities within the resting-state functional images. Anatomical scans were segmented into gray matter, white matter, and cerebrospinal fluid maps and used to remove confounding signal sources associated with white matter and cerebrospinal fluid in the functional data. Functional data was also band-pass filtered from 0.008 to 0.09 Hz.

Functional connectivity was computed between regions of interest (ROIs) within three networks: the language, frontoparietal, and cingulo-opercular network (derived from three regions of the salience network defined in CONN) (see Table 1 for network ROIs and coordinates). Network ROIs were pre-defined in CONN and were derived from an independent component analysis of 497 subjects from the Human Connectome Project (Whitfield-Gabrieli & Nieto-Castanon, 2012). For each participant and each ROI, the time course was averaged across all voxels within the ROI. A bivariate correlation was computed between the average time course of each ROI to every other ROI and Fisher Z-transformed. Within-network connectivity was computed as the average Fisher Z-transform between all ROIs within one network. Between-network connectivity was computed as the average Fisher Z-transformed correlations between all ROIs of one network with all the ROIs of a second network. Within- and between-network connectivity were used as independent variables in statistical analyses (Godwin et al., 2017; Grady, Sarraf, Saverino, & Campbell, 2016).

Table 1. Network and ROI names and MNI center of mass coordinates

	X	Y	Z
Language Network			
L Inferior Frontal Gyrus (IFG)	-51	26	2
R Inferior Frontal Gyrus (IFG)	54	28	1
L Posterior Superior Temporal Gyrus (pSTG)	-57	-47	15
R Posterior Superior Temporal Gyrus (pSTG)	59	-42	13
Cingulo-opercular Network			
Anterior Cingulate Cortex (ACC)	0	22	35
L Anterior Insula	-44	13	1
R Anterior Insula	47	14	0
Frontoparietal Network			
L Prefrontal Cortex (PFC)	-43	33	28
R Prefrontal Cortex (PFC)	41	38	30
L Posterior Parietal Cortex (PPC)	-46	-58	49
R Posterior Parietal Cortex (PPC)	52	-52	45

Statistical analyses

Sentence-picture matching task: Repeated-measures ANOVA and logistic regression were computed using mean RT and accuracy (binary: correct or incorrect) as the dependent variables (DVs), respectively, and the six trial condition types as the independent variables (IVs) to determine main and interaction effects of sentence structure and background noise on sentence comprehension.

Cognitive measures to predict sentence data: Linear regression models were used to predict sentence-picture matching RT and accuracy from working memory and attentional control assessment measures (OST total items recalled and Simon Task incongruent RT – neutral RT, respectively)[1]. Dependent variables in the regression models were RT difference scores from the sentence-picture matching task (e.g. mean RT condition 1 – mean RT condition 2 / mean RT condition 2) instead of mean RT. These difference scores reflect the additional time required to process and respond to the more complex sentence structure or the types of background noise (see Table 2 for a list and brief description of the difference scores). For RT difference scores, a general linear regression model was fit, while for accuracy, a generalized logistic mixed regression model was fit using participants as a random effect. Bivariate correlations to identify potential significant covariates of interest were conducted between the sentence task RT difference scores and the following measures: age, PTA, and WAIS-IV WMI and PSI. Student t-tests were used to determine if sentence task accuracy differed by the covariates of interest. Student t-tests and chi-square tests were used to determine if sentence task RT and accuracy differed by gender, respectively. Only those covariates that significantly correlated with the sentence task DVs were included in subsequent regression models.

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[1] The OST and Simon Task were selected to represent working memory and attentional control abilities, due to their relationships with the cognitive brain networks of interest both in previous literature and in the current dataset. The OST was significantly correlated with functional connectivity within the frontoparietal network (r=.357, *p*=.049), as were several other assessments from the battery (see Appendix A, Table A2). The Simon Task was the only assessment that was significantly correlated with functional connectivity within the cingulo-opercular network (r=-.443, *p*=.013).

Table 2. Categorization of RT difference scores and accuracy by effect of interest

Effect	RT difference scores	Accuracy
Informational masking	Multi-speakers – broadband noise in canonical sentences	Noncanonical sentences in multi-speakers
Energetic masking	Broadband noise – silence in canonical sentences	Noncanonical sentences in broadband noise
Sentence structure	Noncanonical – canonical sentences in silence	Noncanonical sentences in silence
Interactions between masking and structure	Multi-speakers – broadband noise in noncanonical sentences	N/A
	Broadband noise – silence in noncanonical sentences	N/A
	Noncanonical – canonical sentences in multi-speakers	N/A
	Noncanonical – canonical sentences in broadband noise	N/A

RT difference scores computed as mean RT condition 1 – mean RT condition 2 / mean RT condition 2. For the RT difference scores, the level of sentence structure is listed first, followed by the comparison of the levels of background noise. Accuracy is only analyzed in noncanonical structures due to ceiling effects in canonical structures.

Network measures to predict sentence data. Linear and logistic regressions were used to predict sentence-picture matching data from: 1) within-network functional connectivity and 2) between-network functional connectivity measures. The IVs in these models were the language network, frontoparietal network, cingulo-opercular network, language-frontoparietal network and language-cingulo-opercular network functional connectivity. Selection of covariates mirrored the procedure described above. For all procedures described, the statistical significance was defined as an alpha of 0.05, with two-sided alternative hypotheses. Generalized logistic mixed regressions were run in SAS 9.4 and general linear models were run in SPSS 24.

Results

Sentence-picture matching task

Reaction time: Repeated measures ANOVA reveal significant main effects of sentence structure and background noise on participants' mean RT for correct trials only (sentence structure: F(1,30) = 71.20, $p < 0.001$, η = .70; background noise (the assumption of sphericity was violated using Mauchly's test, $\chi^2(2) = 10.62$, $p = 0.005$, therefore Greenhouse-Geisser corrected tests are reported): F(1.53,45.92) = 22.28, *p* < 0.001, η = .43; Figure 1). The interaction effect between sentence structure and background noise was also significant (F(2,60) = 9.72, *p* < 0.001, η = .25). Simple effects and planned pairwise comparisons show that reaction time was impacted by the levels of sentence structure and by background masker (see Table 3). Simple effects indicate that RT increased in the noncanonical conditions compared to canonical. Similarly, simple effects show that RT increased in the presence of background noise, with longer RTs for both multi-speakers and broadband noise compared to silence. However, RT for sentences in multi-speakers was significantly increased compared to broadband noise only for sentences with noncanonical structure; RT between multi-speakers and broadband noise background did not differ within canonical sentence structures.

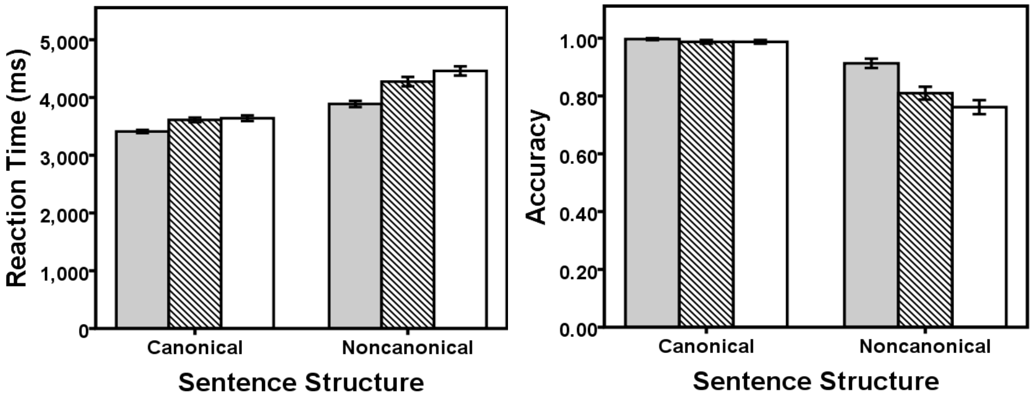

Figure 1. Mean reaction time and accuracy for the sentence-picture matching task. Bars are grouped by the level of sentence structure. Bar color indicates level of background noise. Gray=silence, hatched=broadband, white=multi-speakers.

Table 3. Main and simple effects and pairwise comparisons for reaction time repeated-measures ANOVA in the sentence-picture matching task

		F	df	*p*
Main effect of sentence structure		71.20	30	<.001*
Main effect of background noise		22.28	30	<.001*
Interaction of sentence structure and background noise		9.72	60	<.001*
Simple effect of sentence structure				
Noncanonical > canonical		71.20	30	<.001*
Simple effect of background noise				
Broadband noise > silence		26.26	30	<.001*
Multi-speakers > broadband noise		6.19	30	.019*
Pairwise comparisons		*t*	df	*p*
Effect of informational masking	Canonical: multi-speakers > broadband noise	0.54	30	.590
Effect of energetic masking	Canonical: broadband noise > silence	4.98	30	<.001*

Effect of sentence structure	Noncanonical > canonical: silence	7.79	30	<.001*
Effect of interactions between masker and sentence structure	Noncanonical: multi-speakers > broadband noise	2.52	30	.017*
	Noncanonical: broadband noise > silence	4.36	30	<.001*
	Noncanonical > canonical: multi-speakers	7.71	30	<.001*
	Noncanonical > canonical: broadband noise	6.05	30	<.001*

For pairwise comparisons, the level of sentence structure is listed first, followed by the comparison of the levels of background noise.
*significant at *p*<.05

Accuracy: Logistic regressions of the binary accuracy data revealed a significant main effect of sentence structure ($\chi^2(1) = 14.42$, $p < 0.001$), with noncanonical sentence structures significantly reducing accuracy compared to canonical structures (Z=7.27, $p < 0.001$; Figure 1). The main effect of background noise on accuracy was not significant ($\chi^2(2) = 5.16$, $p = 0.076$) and the interaction of sentence structure and background noise was not significant ($\chi^2(2) = 0.27$, $p = 0.873$).

Models predicting sentence-picture matching data

Linear regression models were conducted to determine the contribution of working memory and attentional control processes to challenging sentence comprehension in older adults. Working memory was measured behaviorally by the OST total items recalled and attentional control was measured by the Simon Test (RT incongruent trials – RT neutral trials); both served as IVs in the models. Linear regression models were also conducted to determine the contribution of brain networks associated with language processing (language network), working memory (frontoparietal network), and attentional control (cingulo-opercular network) to challenging sentence comprehension in older adults. Functional connectivity within the language, working memory, and attentional control networks were used as the IVs. Lastly, linear regression models were analyzed to determine if between-network functional connectivity between the networks associated with working memory and attentional control (frontoparietal and cingulo-opercular, respectively) with the language network contributes to sentence comprehension.

Language-frontoparietal and language-cingulo-opercular network functional connectivity served as the IVs in regression models.

The RT difference scores listed in Table 2 were used as the DVs in these models to represent the additional processing load from the manipulations of sentence structure or background noise. From this point forward, RT will refer to these RT difference scores in Table 2. Accuracy was at ceiling in the canonical sentences (see Figure 1), thus, accuracy at the different levels of background noise within noncanonical sentences served as the DVs in the logistic regression models. Analyses between covariates (e.g. age, PTA, WMI, PSI, and gender), RT, and accuracy determined which covariates to include in each linear regression model and are reported in Table 4. Significant models where the IVs significantly predict RT and accuracy of the effects of background noise and sentence structure are described below and listed in Tables 5-8.

Table 4. Analyses between sentence task data and covariates for inclusion in linear regression models

		Age	PTA	WMI	PSI	Gender
RT difference scores						
Effect of informational masking	Canonical: multi-speakers – broadband noise	*r* = -.06	*r* = .05	*r* = -.31	*r* = -.42*	*t* = 1.40
Effect of energetic masking	Canonical: broadband noise –silence	*r* = .08	*r* = .52*	*r* = -.11	*r* = -.23	*t* = -.08
Effect of sentence structure	Silence: Noncanonical - canonical	*r* = -.06	*r* = -.11	*r* = -.05	*r* = -.33	*t* = -1.40
Interaction of masker and structure	Noncanonical: multi-speakers – broadband noise	*r* = .06	*r* = .36*	*r* = -.13	*r* = -.05	*t* = .97
	Noncanonical: broadband noise – silence	*r* = .49*	*r* = .37*	*r* = .07	*r* = .04	*t* = -.61
	Multi-speakers: Noncanonical – canonical	*r* = .35	*r* = .28	*r* = .12	*r* = .10	*t* = -1.07
	Broadband noise: Noncanonical – canonical	*r* = .34	*r* = .02	*r* = .09	*r* = -.09	*t* = -1.43
Accuracy						
Effect of informational masking	Noncanonical in multi-speakers	*t* = 1.68	*t* = 2.20*	*t* = -3.32*	*t* = 1.12	χ^2 = .03
Effect of energetic masking	Noncanonical in broadband noise	*t* = 0.15	*t* = 1.45	*t* = -4.46*	*t* = -1.06	χ^2 < .001
Effect of sentence structure	Noncanonical in silence	*t* = 4.47*	*t* = 3.07*	*t* = -4.80*	*t* = -1.06	χ^2 = 8.16*

Analysis of RT difference scores with continuous covariates relied on Pearson correlations; analysis of RT difference scores with gender relied on the Student t-test; analysis of accuracy with continuous covariates relied on the Student t-test; analysis of accuracy with gender relied on the Chi-square test.
*significant at $p<.05$

Effect of informational masking: The model examining the effect of informational masking by predicting RT of canonical sentences in multi-speakers compared to broadband noise from behavioral measures was significant ($R^2 = .26$, $p = 0.041$). However, the only significant predictor was PSI (ß = -.42, $p = 0.030$), whereas the OST (ß = -.12, $p = 0.507$) and Simon Task (ß = -.28, $p = 0.114$) were not significant predictors. This same model predicted by within-network functional connectivity was significant ($R^2 = .37$, $p = 0.016$). In this model, PSI (ß = -.44, $p = 0.012$) and frontoparietal network connectivity (ß = -.36, $p = 0.040$) were significant predictors, but not language (ß = .30, $p = 0.146$) or cingulo-opercular network connectivity (ß = .12, $p = 0.667$). The RT model with between-network functional connectivity was also significant ($R^2 = .38$, $p = 0.005$), with PSI (ß = -.49, $p = 0.004$) as the strongest predictor, followed by language-frontoparietal connectivity (ß = -.37, $p = 0.026$). Language-cingulo-opercular functional connectivity was not significant (ß = .18, $p = 0.251$).

For accuracy of noncanonical sentences in multi-speakers, the model examining this effect via behavioral measures was significantly predicted by the covariates age (ß = -.85, $p = 0.001$) and WMI (ß = .77, $p = 0.012$). The covariates PTA (ß = -.20, $p = 0.317$) and gender (ß = -.57, $p = 0.310$) and IVs Simon Task (ß = .34, $p = 0.125$) and OST (ß = -.13, $p = 0.696$) were not significant predictors in this model. However, the accuracy effect of informational masking from within-network functional connectivity was significantly predicted by WMI (ß = .79, $p < 0.001$) and within-network frontoparietal connectivity (ß = .66, $p = 0.016$). Age (ß = -.53, $p = 0.066$), PTA (ß = -.08, $p = 0.652$), gender (ß = .30, $p = 0.627$), language network connectivity (ß = -.40, $p = 0.151$), and cingulo-opercular network connectivity (ß = -.19, $p = 0.411$) were not significant predictors. The model predicting this effect from between-network functional connectivity was significantly predicted by the covariates WMI (ß = .79, $p = 0.001$) and age (ß = -0.66, $p = 0.012$). However, PTA (ß = -0.15, $p = 0.441$), gender (ß = .60, $p = 0.569$) and between language-cingulo-opercular connectivity (ß = -23, *p* = 0.261) and language-frontoparietal connectivity (ß = 0.12, *p* = 0.612) were not significant predictors.

Effect of energetic masking: For canonical sentences, the model examining the effect of energetic masking by predicting RT in broadband noise compared to silence was significant (R^2 = .40, *p* = 0.003). PTA (ß = .50, *p* = 0.004) and the OST (ß = -.35, *p* = 0.031) were significant predictors but not the Simon Task (ß = -.14, *p* = 0.384). The model predicting energetic masking from within-network connectivity was significant (R^2 = .34, *p* = 0.026). This effect was significantly predicted by PTA (ß = .53, *p* = 0.003) but no measure of within-network connectivity (language connectivity: ß = -.29, *p* = 0.156; frontoparietal connectivity: ß = .03, *p* = 0.880; cingulo-opercular connectivity: ß = .23, *p* = 0.234). The model predicting the RT of energetic masking from between-network functional connectivity was significant (R^2 = .29, *p* = 0.025), however only PTA (ß = .52, *p* = 0.004) was a significant predictor (language-frontoparietal: ß < .01, *p* = 0.997; language-cingulo-opercular: ß = .12, *p* = 0.482).

In the model predicting accuracy for noncanonical sentences in broadband noise from behavioral measures, only WMI significantly predicted accuracy (ß = .47, *p* = 0.041). The Simon Task was not a significant predictor (ß = .30, *p* = 0.071) nor was the OST (ß = .30, *p* = 0.164). The model predicting accuracy from within-network functional connectivity was not significantly predicted by within-network connectivity (language: ß = .32, *p* = 0.174; frontoparietal: ß = -.13, *p* = 0.609; cingulo-opercular: ß = -.33, *p* = 0.113), only the covariate WMI was a significant predictor (ß = .65, *p* < 0.001). Predicting this effect with between-network functional connectivity, WMI was the only significant predictor (ß = 0.67, *p* = 0.003). The between language-cingulo-opercular network functional connectivity was not significant (ß = -0.12, *p* = 0.625), and the language-frontoparietal functional connectivity was also not significant (ß = -.08, *p* = 0.763).

Effect of sentence structure: The RT effect of sentence structure was not significantly predicted by the covariates, cognitive measures of working memory and attentional control, within-network, or between-network functional connectivity measures.

However, in the model predicting the accuracy effect of sentence structure (noncanonical sentences in silence) from behavioral measures, the Simon Task was the strongest, significant predictor (ß = .50, *p* = 0.031), followed by the OST (ß = .47, *p* = 0.034). The covariates were not significant predictors of accuracy (PTA: ß = -.45, *p* = 0.085, WMI: ß = .38, *p* = 0.237). Similarly, the model predicting accuracy of noncanonical sentences in silence was significantly predicted by the cingulo-opercular within-network connectivity (ß = -.91, *p* = 0.001), WMI (ß = .68, *p* = 0.002), and PTA (ß = -.37, *p* = 0.047), but not by language connectivity (ß = .12, *p* = 0.537) or frontoparietal connectivity (ß = .14, *p* = 0.630). Lastly, in the model predicting accuracy for noncanonical sentences in silence from between-network functional connectivity, WMI was the only significant predictor (ß = 0.74, *p* = 0.017). PTA (ß = -0.38, *p* = 0.4134); language-cingulo-opercular network functional connectivity (ß = -0.15, *p* = 0.644), and language-frontoparietal network functional connectivity (ß = .17, *p* = 0.421) were not significant.

Interaction effects of masker and sentence structure: The models predicting the RT effect of informational masking in noncanonical sentences from behavioral measures, within-network and between-network functional connectivity were not significant.

The model testing the RT effect of energetic masking in noncanonical sentences from behavioral measures was significant (R^2 = .33, *p* = 0.031), but only age (ß = .47, *p* = 0.018) was a significant predictor. In this model PTA (ß = .27, *p* = 0.132), OST (ß = -.06, *p* = 0.721), and the Simon Task (ß = -.20, *p* = 0.274) were not significant predictors. Similarly, the model of RT effect of energetic masking in noncanonical sentences predicted by between-network functional connectivity was significant (R^2 = .33, *p* = 0.029), but only age (ß = .36, *p* = 0.047) was a significant predictor; PTA (ß = .26, *p* = 0.134); language-frontoparietal connectivity (ß = -.21, *p* = 0.225), and language-cingulo-opercular functional connectivity (ß = -.04, *p* = 0.796) were not significant predictors. This model was not significantly predicted by within-network functional connectivity either.

Models predicting the interactive effects of sentence structure (noncanonical – canonical) in the presence of different maskers (broadband noise and multi-speakers) were not significantly predicted by any covariate, behavioral measure, or within- or between-network functional connectivity.

Table 5. Significant regression models of the effect of informational masking

RT difference score	ß	*p*
Canonical: multi-speakers – broadband noise		
Within-network predictors		
PSI	-.44	.012*
Language connectivity	.30	.146
Frontoparietal connectivity	-.36	.040*
Cingulo-opercular connectivity	.12	.667
Between-network predictors		
PSI	-.49	.004*
Language-frontoparietal connectivity	-.37	.026*
Language-cingulo-opercular connectivity	.18	.251
Accuracy	ß	*p*
Noncanonical: multi-speakers		
Within-network predictors		
PTA	-.08	.652
Age	-.53	.066
WMI	.79	<.001*
Gender	.30	.627
Language connectivity	-.40	.151
Frontoparietal connectivity	.66	.016*
Cingulo-opercular connectivity	-.19	.411

For each regression model, the level of sentence structure is listed first, followed by the comparison of the level of background noise. PTA=pure tone average; PSI=processing speed index; OST=operation span task; WMI=working memory index.
*significant at *p*<.05

Table 6. Significant regression models of the effect of energetic masking

RT difference score	ß	*p*
Canonical: broadband noise – silence		
Cognitive predictors		
PTA	.50	.004*
OST	-.35	.031*
Simon Task	-.14	.384

For each regression model, the level of sentence structure is listed first, followed by the comparison of the level of background noise. PTA=pure tone average; OST=operation span task.
*significant at *p*<.05

Table 7. Significant regression models of the effect of sentence structure

Accuracy	ß	*p*
Noncanonical: silence		
Cognitive predictors		
PTA	-.45	.085
WMI	.38	.237
OST	.47	.034*
Simon Task	.50	.031*
Within-network predictors		
PTA	-.37	.047*
WMI	.68	.002*
Language connectivity	.12	.537
Frontoparietal connectivity	.14	.630

Cingulo-opercular connectivity	-.91	.001*

For each regression model, the level of sentence structure is listed first, followed by the level of background noise. PTA=pure tone average; WMI=working memory index; OST=operation span task.
*significant at *p*<.05

Discussion

The aim of the present study was to determine the contributions of working memory and attentional control to speech comprehension in difficult conditions in older adults. Previous separate investigations into the neurobiological resources recruited in response to sentences with complex structures and background noise often identify increased activation in brain regions corresponding to the frontoparietal and cingulo-opercular networks, respectively. However, it is not clear if the cognitive resources known to be recruited by speech with complex sentence structures and in difficult listening environments are the same or distinct, nor how hearing loss impacts the recruitment of these resources. In this study, cognitive assessments and resting-state fMRI were used to investigate brain networks associated with working memory and attentional control to predict speech comprehension of structurally and acoustically complex stimuli, after controlling for hearing loss in older adults. The results indicate that increased functional connectivity of the frontoparietal network is related to improved comprehension of sentences in multi-speakers. Comprehension of sentences in broadband noise was not related to any of the functional connectivity measures but was significantly predicted by behavioral measures of working memory. Comprehension of sentences with complex structures was most strongly predicted by behavioral measures of attentional control and the functional connectivity of the cingulo-opercular network. These findings describe the distinct ways in which behavioral measures and brain networks associated with working memory and attentional control are involved in auditory speech comprehension in older adults after accounting for hearing loss.

Resources supporting sentence comprehension in background noise

These findings consistently implicate the involvement of the frontoparietal network in older adults' comprehension abilities of speech in multi-speakers (i.e. informational masking). The regression models testing this effect identify both functional connectivity between the frontoparietal and language networks and functional connectivity within the frontoparietal network as significant predictors of comprehension abilities. These findings suggest that increased functional connectivity, either between the frontoparietal and language networks or within the frontoparietal network, leads to better comprehension of speech in multi-speaker backgrounds.

The relationships between functional connectivity and sentence comprehension described above were significant even after controlling for several covariates. In the models of the RT effect of informational masking, processing speed was the strongest predictor (i.e. had the largest beta weight) and was negatively correlated with RT, indicating that better speech comprehension was related to faster processing speed scores. Whereas in the model predicting accuracy for noncanonical sentences in multi-speakers, the working memory index (a measure of simple working memory) was the strongest predictor, indicating that accurate speech comprehension was related to increased simple working memory abilities, as some studies have previously reported (Humes, 2007; van Rooij & Plomp, 1990). Other studies do implicate complex working memory (e.g. span tasks) in sentence comprehension (for reviews see Arlinger, Lunner, Lyxell, & Kathleen Pichora-Fuller, 2009; Peelle, 2018), but the present study did not find that complex working memory (the OST) significantly predicted informational masking. However, it was found that functional connectivity of the frontoparietal network was also a significant predictor of the effect of informational masking, suggesting that the functional integrity of the frontoparietal network also contributes to improved speech in multi-speaker comprehension abilities in older adults.

While the exact cognitive functions supported by the frontoparietal network are still debated, prominent theories propose that this network is involved in initiating and adapting attentional control during a task (Dosenbach et al., 2007) and in top-down direction of attention toward stimuli from the environment as it relates to internal or task goals (Seeley et al., 2007; Wallis, Stokes, Cousijn, Woolrich, & Nobre, 2015). Supporting these functions, activation within brain regions constituting the frontoparietal network (bilateral dorsolateral prefrontal and posterior parietal cortex) is frequently observed in studies of working memory (Cole & Schneider, 2007;

D’Esposito & Postle, 2015; Lara & Wallis, 2015). The attentional control and working memory functions of this network are also implicated in the ELU model of auditory speech comprehension, serving to respectively select the target speech signal from among competing background signals and hold a misheard signal in working memory for further processing (Rönnberg et al., 2013). Therefore, these findings suggest that processing speech in multi-speaker backgrounds in older adults is sustained by the functional integrity of the frontoparietal network and the attentional control and working memory processes that it supports.

Activation in prefrontal regions that fall within the frontoparietal network has been reported in some studies of language processing in older adults and is commonly attributed to working memory or other compensatory processes, but these findings only come from studies of complex sentence structures, not in acoustically challenging speech (Grossman et al., 2002; Peelle et al., 2009; Tyler et al., 2009). Several task-based fMRI studies comparing acoustically challenging to clear spoken sentences report increased activation within the cingulo-opercular network (Adank, 2012; Erb et al., 2013; Erb & Obleser, 2013). However, this study did not find any significant relationship between the functional connectivity of the cingulo-opercular network and measures of language comprehension in multi-speaker backgrounds. It is possible that the intrinsic functional integrity of the cingulo-opercular network is not an important factor in comprehension of speech in noisy environments *per se*, but that the responsivity of the regions within this network during online speech processing is critical to comprehension of speech in multi-speaker backgrounds.

It should be noted that hearing ability was not included as a covariate in the models of informational masking because it did not significantly correlate with the comprehension measure of informational masking, i.e. RT difference of canonical sentences in multi-speakers and canonical sentences in broadband noise. Both conditions contain additional acoustic information on top of the target speaker, but only the sentences with the multi-speaker background contain an additional cognitive load from the presence of additional speech (i.e. informational masking). However, hearing ability did significantly correlate with the RT effect of energetic masking (as seen in Table 6). This suggests that hearing ability significantly predicts comprehension of speech in noisy environments more generally, as previously reported (Humes, 2008; Pichora-Fuller & Souza, 2003; Schneider et al., 2002), but that hearing may not relate to the ability to successfully understand the target speaker from multi-speaker backgrounds specifically.

The energetic masking models yielded notably different results than those for information masking. Neither within- nor between-network functional connectivity significantly predicted comprehension abilities of speech in broadband noise compared to in silence (i.e. energetic masking). The strongest predictor of the RT effect of energetic masking was hearing abilities, revealing that poorer hearing correlated with worse comprehension abilities. However, performance on the OST, a behavioral measure of complex working memory, was the other significant predictor after hearing abilities, such that better working memory was associated with better comprehension abilities for speech in broadband noise. This finding suggests that the ability to comprehend speech signals that are acoustically degraded, but that do not necessarily contain additional speech information, is dependent upon both hearing and complex working memory abilities. In response to a misheard speech signal, the proposed role of working memory is to maintain the acoustic speech signal in memory while the rest of the utterance unfolds, so that additional context or rehearsal may clarify the misheard signal (Peelle, 2018; Rönnberg et al., 2008).

Collectively, these findings support the role of complex working memory in the comprehension of acoustically challenging spoken language in older adults, as proposed by the ELU model, but only in the presence of energetic and not informational masking. Instead, this study suggests that informational masking is supported by simple working memory. This study further provides evidence for the role of the frontoparietal network and the strength of its functional connectivity to the language network in supporting acoustically challenging spoken language comprehension in older adults. This relationship is specific to the comprehension of speech with informational masking, and not in overcoming acoustic degradation more generally (as with energetic masking).

Resources supporting comprehension of sentences with complex structures

No regression models predicting RTs of sentence structure from cognitive or network connectivity measures were significant. Accuracy was at ceiling for most participants for sentences with canonical structures, thus only the accuracy of sentences with noncanonical structures was investigated in the regression models. These findings reveal that better complex working memory (as measured by the OST) was associated with higher comprehension accuracy for sentences with noncanonical structures without background noise, in line with other previous studies of comprehension of complex sentence structures in older adults (Goral et al., 2011; Just & Carpenter, 1992; Norman et al., 1992).

Conversely, it was found that poorer attentional control (as reflected in increasing Simon Task scores) was significantly correlated to increased accuracy in comprehending sentences with noncanonical structures and was a stronger predictor than working memory, even after controlling for hearing and simple working memory abilities. This relationship between poorer attention and better sentence comprehension is unexpected, but a previous study has reported a similar finding for sentences presented in broadband noise. Knight & Heinrich (2017) investigated measures of inhibition (one aspect of attentional control) derived from two Stroop tasks and found a similar inverse relationship between attentional control and speech in noise comprehension in older adults. The authors suggest that performance scores derived from reaction time in Stroop tasks (and by extension, the Simon Task) may not be reliable in older adults, instead reflecting age differences in processing speed declines or in response strategy. Thus, the negative correlation between attentional control abilities and speech comprehension in this study may too be driven by differences in processing speed or response strategies. When Knight & Heinrich (2017) separated the RTs in the Stroop task into bins and analyzed only the fastest RTs, better inhibition scores predicted better comprehension, whereas for trials with the slowest RTs, poorer inhibition scores predicted better comprehension, suggesting that older adults exhibit inconsistent response strategies.

In this study, significant negative correlations were observed between average accuracy and reaction time on the Simon Task for both congruent and neutral trials (r=-.470, p=0.008 and *r*=-.497, *p*=0.004, respectively), indicating that longer reaction times resulted in poorer accuracy during the task in the congruent and neutral trial types. However, this relationship between accuracy and reaction time was not present in the incongruent trials (*r*=-.176, *p*=0.344), suggesting that the older adults in this study also applied different response strategies during the attention-demanding incongruent trials of the Simon Task than in the congruent and neutral trials. Other studies report that older adults favor response accuracy over speed (Brébion, 2001; Smith & Brewer, 1995; Starns & Ratcliff, 2010). It is possible that increased Simon Task scores (i.e. RT for incongruent trials – RT for neutral trials) do not necessarily represent poorer attentional control ability but instead represent a more careful approach to response selection in response to increased cognitive demands. Thus, participants who adopted this more careful approach in the Simon Task may have performed equally as carefully in response to complex, noncanonical sentence structures, resulting in higher accuracy. Similar differences in response strategy to attentional control tasks in older adults have been reported elsewhere (Geerligs, Saliasi, Maurits, Renken, & Lorist, 2014; Rush, Barch, & Braver, 2006; Sebastian et al., 2013) However, more studies into age-related changes in speed-accuracy tradeoffs and how they may influence the interpretation of attentional control abilities in older adults are needed.

This study also found that functional connectivity of the cingulo-opercular network significantly predicted comprehension of complex sentence structures, albeit in the opposite direction as expected. Previous studies have linked this network to top-down control of task maintenance (Dosenbach et al., 2007; Eckert et al., 2009; Petersen & Posner, 2012) and sustained alertness (Coste & Kleinschmidt, 2016). Others have identified activation in this network in response to conflicting stimuli, likely as a proxy for task difficulty and cognitive effort (Botvinick, Cohen, & Carter, 2004). This study found that increased connectivity within the cingulo-opercular network significantly correlated with decreased accuracy for sentences with complex structures. This finding may correspond to the same rationale derived from the Simon Task findings described above. As stated in the methods, the Simon Task was the only cognitive measure that significantly correlated with cingulo-opercular within-network functional connectivity (*r*=-.443, *p*=0.013), such that increased within-network connectivity was associated with "better" attentional control abilities (i.e. decreased Simon Task scores). However, if increased Simon Task scores instead reflect a careful response strategy, then decreased cingulo-opercular within-network functional connectivity is associated with this more careful response strategy. Therefore, participants expressing decreased cingulo-opercular within-network connectivity may utilize a more careful response approach, leading to higher accuracy in the comprehension of structurally complex sentences.

Other studies investigating changes in network connectivity with age report that older adults exhibit reduced functional connectivity (i.e. connectivity becomes more negative) within in the cingulo-opercular network compared to younger adults (Geerligs et al., 2015; Meier et al., 2012). Notably, one of these studies also reported that decreased functional connectivity within the cingulo-opercular network was correlated with increased working memory performance in younger adults and increased crystallized intelligence performance (defined by the Trail Making Test and National Adult Reading Test) in older adults (Geerligs et al., 2015). While the behavioral and cognitive significance of decreased functional connectivity of the cingulo-opercular network with age is not well studied, these findings coincide with this study’s finding that decreased functional connectivity can be associated with better cognitive performance.

To summarize, cingulo-opercular network functional connectivity was the strongest predictor of comprehension of complex sentence structures, over other significant predictors including hearing and simple working memory abilities. The involvement of the cingulo-opercular network implicates attentional control in the comprehension of sentences with noncanonical structures, however an interpretation of the directionality of these relationships is unclear and requires further study.

Conclusion

In the present study, the contributions of working memory and attentional control to difficult sentence comprehension were investigated using behavioral measures and resting-state fMRI measures of network functional connectivity. Critically, covariates for several possible aging-related confounds were included, such as hearing ability, processing speed, and age. Increased functional connectivity between the frontoparietal and language brain networks, and increased connectivity within the frontoparietal network, were associated with better comprehension of sentences in multi-speaker backgrounds. It was further demonstrated that the contributions of the frontoparietal network are specific to speech in multi-speaker environments (i.e. informational masking), and not to acoustic degradation more general (i.e. energetic masking). Similarly, these data suggest that better hearing and complex working memory abilities in older adults are associated with better speech comprehension with energetic masking, but not with informational masking. Informational masking was instead supported by simple working memory. Lastly, attentional control may be implicated in comprehending sentences with complex, noncanonical structures, however further research into age-related changes in attentional control and in speed-accuracy tradeoffs are needed to clarify these findings. Together these findings indicate that in older adults, working memory and the frontoparietal network support comprehension of speech in background noise after controlling for hearing loss, whereas attentional control and the cingulo-opercular network are involved in parsing complex sentence structures.

CHAPTER 4

EXPERIMENT 3: BRAIN ACTIVATION TO CHALLENGING AUDITORY SPEECH COMPREHENSION IN OLDER ADULTS: DIFFERENCES DUE TO HEARING LOSS, WORKING MEMORY, AND ATTENTIONAL CONTROL

Introduction

A large portion of older adults experience communication difficulties in their daily lives (Committee on Hearing, Bioacoustics, and Biomechanics, 1988; Hamilton-Wentworth District Health Council, 1988). As discussed in Experiment 2, older adults experience comprehension declines in response to rapid speech, sentences with complex structures, and speech in noisy environments (Caplan et al., 2011; Helfer et al., 2017; Kemtes & Kemper, 1997; Jonathan E. Peelle et al., 2009; Rajan & Cainer, 2008; Ward et al., 2016). Previous studies have contributed such comprehension deficits in older adults to age-related hearing loss (Pichora-Fuller & Souza, 2003; Schneider et al., 2002). However, others suggest that cognitive abilities also influence auditory speech comprehension in older adults (Akeroyd, 2008; Anderson et al., 2013; Besser et al., 2015; Desjardins & Doherty, 2013; Humes, 2007).

The findings from Experiment 2 support the involvement of cognitive abilities in speech comprehension: complex and simple working memory were implicated in different aspects of speech in noise comprehension and attentional control was related to comprehension of complex sentence structures. Experiment 2 further concluded that the resting-state functional connectivity of the frontoparietal and cingulo-opercular networks predict speech in noise and complex sentence structure comprehension abilities, respectively. However, to have a more complete understanding of how these cognitive resources contribute to sentence comprehension, it is also critical to investigate activations in response to speech stimuli to identify the regions engaged during challenging auditory speech comprehension.

Numerous functional neuroimaging studies have characterized the neurobiology of language processing in younger adult populations and identify several brain regions that have increased activation in response to auditory speech stimuli compared to a variety of acoustically-matched control conditions. These studies identify a bilateral fronto-parieto-temporal network that includes bilateral superior and middle temporal gyri, inferior parietal regions (e.g. angular gyrus and supramarginal gyrus), anterior temporal cortex, and the left inferior frontal gyrus (i.e. Broca's area) (Binder et al., 2000; Friederici, 2012; Hickok & Poeppel, 2007; Rauschecker & Scott, 2009; Rogalsky & Hickok, 2009; Tyler & Marslen-Wilson, 2008). However, studies of comprehension in older adults compared to younger adults reveal reduced activation within Broca's area and increased activation outside of typical, speech comprehension regions, including right frontal cortex and bilateral parietal cortex in response to complex sentence structures (Peelle et al., 2009; Tyler et al., 2009). In addition, previous work has found reduced activation in right primary auditory cortex (i.e. Heschl's gyrus) and increased activation in bilateral middle frontal and inferior parietal regions in response to speech in noise in older compared to younger adults (Eckert, Walczak, et al., 2008; Wong et al., 2009). The cingulo-opercular network is also thought to be involved in processing speech in noise (Erb & Obleser, 2013; Vaden et al., 2015) Lastly, age-related hearing loss is associated with reduced activation within Heschl's gyrus in response to auditory sentences (Peelle et al., 2011).

These findings mirror several models of cognitive brain aging which posit that differences in the brain's response to a variety of task-related cognitive processes in older adults compared to younger adults reflects compensatory mechanisms in an attempt to maintain sufficient task performance (for a review of these models, see Grady, 2012). However, it is unclear if the additional frontal and parietal regions recruited in response to auditory speech comprehension in older adults reflects response-related processes also typically observed in frontal and parietal regions (Hall et al., 2000); the studies described above used task-based paradigms that required participants to either respond to a prompt via button press (e.g. a post-stimulus comprehension probe) or by verbally repeating the presented word or sentence. Active tasks such as these likely recruit top-down cognitive resources that are necessary for performing the task (e.g. memory for the directions, response selection, etc.) but that are not necessarily involved in language comprehension *per se* (Crinion, Lambon-Ralph, Warburton, Howard, & Wise, 2003; Noesselt, Shah, & Jäncke, 2003). It is also unclear how the engagement of these brain regions outside of the traditionally-defined auditory speech comprehension network is related to comprehension ability.

The present study used a passive-listening fMRI paradigm to identify the brain regions activated during challenging auditory sentence comprehension in older adults, and how these activations may be related to sentence comprehension performance measured outside of the MRI scanner. The paradigm was designed to more closely capture the brain regions involved in comprehension than previous studies because: 1) sentence stimuli varied in their level of sentence structure complexity and background noise, combining effects that were previously studied independently; and 2) a passive paradigm was selected in order to identify the brain regions involved in naturally listening to and comprehending speech in the absence of induced, task-related effects. Critically, this study explored how activation in response to challenging auditory speech comprehension is altered by hearing loss and related to an individual's working memory and attentional control abilities.

It is expected that comprehending auditory sentences in general will engage bilateral superior temporal and left inferior frontal regions. Comparisons of complex sentence structures to more simple structures will reveal increased activation within bilateral inferior frontal gyrus, right middle and superior frontal gyri, and right inferior parietal regions (portions of which overlap with the frontoparietal network explored in Experiment 2), whereas speech in a multi-talker backgrounds compared to speech without background talkers will elicit activation within the dorsal anterior cingulate and bilateral insula (coinciding with the cingulo-opercular network from Experiment 2). It is further predicted that hearing loss will result in decreased activation in Heschl's gyrus and corresponding increased activation outside of typical auditory speech comprehension regions, including frontoparietal network regions, and that such increases will be related to comprehension ability. Lastly, it is expected that individuals with better working memory abilities will recruit regions within the frontoparietal network and, similarly, those with better attentional control abilities will recruit regions within the cingulo-opercular network in response to challenging sentence comprehension, and that these increases will predict better comprehension ability.

Methods

Participants

Twenty-seven of the 31 older adult participants in Experiments 1 and 2 also participated in the present study. Five of the 31 participants from the previous experiments were excluded in this experiment due to the presence of an fMRI artifact within the passive-listening paradigm, resulting in poor data quality. Participants were aged 60 to 80 years (17 women; mean(sd) age = 67.96(5.64) years, mean(sd) education = 17.44(3.22) years) and met the same inclusion criteria as experiment 1. Pure-tone audiometry was used to determine participant hearing ability (i.e. pure-tone average, PTA) using the procedure described in Experiment 1 (PTA mean(sd) = 27.02(12.37), range: 6.25 – 52.93 dB). If the participant wore hearing aids, the language comprehension task was performed aided, while pure-tone audiometry and MRI were collected unaided. Hearing ability did not significantly correlate with participant age ($r = 0.288$, $p = 0.145$). Written informed consent was obtained from each participant in accordance with Arizona State University's Institutional Review Board guidelines. Participants were compensated monetarily for their efforts.

Language comprehension

The same sentence-picture matching task described in Experiment 2 was used as the measure of auditory sentence comprehension. Sentences varied in their level of sentence structure complexity (canonical and noncanonical) and background noise (silence, broadband noise, and multi-speakers). Dependent variables from this task were the RT difference scores that reflect the additional, cognitive processing time to respond to speech in informational and energetic masking, and the interaction of sentence structure and masking, as outlined in Experiment 2 (Table 1).

Table 1. Categorization of RT difference scores and accuracy by effect of interest

Effect	RT difference scores
Informational masking	Multi-speakers – broadband noise in canonical sentences
Energetic masking	Broadband noise – silence in canonical sentences
Sentence structure	Noncanonical – canonical sentences in silence
Interactions between masking and structure	Multi-speakers – broadband noise in noncanonical sentences
	Broadband noise – silence in noncanonical sentences
	Noncanonical – canonical sentences in multi-speakers
	Noncanonical – canonical sentences in broadband noise

RT difference scores computed as mean RT condition 1 – mean RT condition 2 / mean RT condition 2. For the RT difference scores, the level of sentence structure is listed first, followed by the comparison of the levels of background noise. Accuracy is only analyzed in noncanonical structures due to ceiling effects in canonical structures.

Cognitive measures

Scores from the Operation Span Task (OST) and the Simon Task, as described in Experiment 2, were used as measures of working memory and attentional control abilities, respectively.

MRI methodology

All scanning was conducted at the Barrow Neurological Institute in Phoenix, AZ on a research-dedicated 3T Phillips Ingenia scanner. A single-shot echo-planar imaging (EPI) pulse sequence was used to measure changes in the blood-oxygenation level dependent (BOLD) signal. Visual stimuli were presented using Nordic Neurolab's MR-compatible high-resolution LED goggles and auditory stimuli were presented using MR-compatible headphones. E-Prime Standard 2.0 software on a Dell PC laptop presented stimuli. Resting-state fMRI were also collected from these participants in the same session (as described in Experiments 1 and 2).

A passive-listening paradigm using the same sentence stimuli from the sentence-picture matching task was developed to assess brain activation in response to spoken sentence comprehension using fMRI. A clustered sparse-sampling pulse sequence was used. This sequence inserts a delay between clusters of volume acquisitions such that auditory stimuli can be presented between acquisition periods in relative silence. Sparse sampling is recommended for studies with auditory stimuli as it reduces interference from scanner noise and variance in auditory cortex activation, thus increasing the signal-to-noise ratio (Hall, 1999). Furthermore, the “clustered” aspect of this sequence acquired three volumes per stimuli, increasing the number of BOLD signal time points captured in response to each sentence (Perrachione 2013; Peelle 2014). The imaging sequence for this paradigm was as follows: TR=13.33s for three volumes and stimulus delivery, TA=2.66s for single volume (8s for the three volumes), stimulus presentation window=5.33s, TE=30, flip angle=90, FOV= 200 x 200, matrix=80 x 79, 36 ascending axial slices covering the whole cortex, slice thickness=3mm, in-plane resolution=2.5 x 2.5mm, total scan time 6 minutes and 13 seconds.

Sentences from experiment 2 were presented during fMRI acquisition. Sentences contained one of two levels of sentence structure (canonical or noncanonical) and were presented in one of two levels of background noise (silence or multi-speakers). The broadband noise background used in Experiment 2 was excluded in this paradigm to increase the number of trials in the other conditions. Sparse sampling protocols have reduced power compared to continuous scanning of the same duration due to the gaps in volume acquisition, thus I chose to maximize trials in the other conditions of interest while still maintaining a reasonable total scanning time for the older adult participants. This was a passive listening paradigm, so no pictures were presented, and no responses were required; participants were instructed to listen to the sentences and to focus on the target speaker when sentences were presented in background noise. Prior to scanning, participants listened to several samples of sentences both with and without background noise to learn the target speaker’s voice. The paradigm was completed over four fMRI runs. Each of the four runs had 25 trials, with five trials each for the four sentence conditions and five null trials (i.e. no auditory stimuli presented, fixation cross present). The trials were randomly presented without replacement for a total of 20 trials per condition over the four runs. Each trial began with the presentation of the auditory sentence stimulus in the presence of a visual fixation cross. Sentence stimuli were presented in an approximately 5 second (s) window. Next, 3 volumes were acquired (8 s); the fixation cross remained on the screen. The remaining time was silent and served to jitter the onset of the next trial (between approximately 100-500 milliseconds).

A high-resolution T1 anatomical scan was also acquired for each participant. The imaging parameters were as follows: MPRAGE sequence, TR=6.74s, TE=3.10ms, flip angle=9°, FOV=270 x 253, matrix=256x256, voxel size=1.1 x .1.1 x 1.2mm, 170 sagittal slices, acquisition time =5 minutes 34 seconds.

FMRI data pre-processing

Statistical Parametric Mapping 12 (SPM 12; Wellcome Institute of Cognitive Neurology, London, UK) was used to reconstruct the functional images. MRIcron (Rorden, Brett 2000) was used to reconstruct the structural images. Image pre-processing and analysis was conducted using Analysis of Functional Neuroimages (AFNI; http://afni.nimh.nih.gov/afni). The first volume from each run was removed to allow for the longitudinal magnetization to reach an equilibrium. Motion correction was applied to all EPI images, aligning images to the last volume of the fourth run, since the T1 was collected immediately following this volume (Cox, 1999). The T1 image was then aligned to this volume using AFNI's "align_epi_anat.py" program. A Gaussian smoothing kernel of 6mm full-width, half maximum (FWHM) was applied to the functional images to aid in group-level analyses. A voxel-wise general linear model was applied using regressors for the onset time and duration of each sentence in each condition. Additional regressors included the grand mean of the BOLD signal, the six motion parameters, and two regressors reflecting the signal intensity decay across the three acquired volumes per trial (Schmidt et al., 2007, Zaehle et al., 2007). Regressors were convolved with a standard hemodynamic response function, creating predictor variables for the analysis. An F-statistic was computed for each voxel, creating statistical maps that identify voxels with an increased BOLD response for the selected condition compared to the null trials (i.e. no stimuli presented) and between conditions of interest. Each participant's anatomical image was transformed into Talairach space in AFNI by aligning the AC-PC plane and anatomical markers and scaling the brain to the Talairach-Tourneaux atlas. The statistical maps were transformed into Talairach space and resampled into 2x2x2mm voxels using AFNI's "adwarp" program.

FMRI data analysis

Group voxel-wise t-tests were performed with AFNI's 3dttest++ program to characterize activations in response to each sentence condition compared to the null trials. 3dttest++ also was used to compute contrasts reflecting the main effects of sentence structure and masker, as well as follow-up simple comparisons between levels of sentence structure and masker (described in the next paragraph). Since this experiment did not include sentences in broadband noise, the contrast representing the effect of masking reflects both informational and energetic masking. The -ETAC option of AFNI's 3dttest++ program was used to threshold statistical maps at a voxel-wise false positive rate (FPR) of 5% (Cox, 2018). This method of multiple comparisons correction performs iterative statistical tests across a range of commonly-used thresholds (p<0.01, 0.005, and 0.001, in this study) while maintaining an FPR of 5%. Critically, this method does not assume homogenous spatial noise across the brain, instead estimating the random noise within the data to determine significant cluster size thresholds across the brain. A voxel is considered significant if it passes any of the iterative tests. This method allows for the detection of large clusters of low effect size and smaller clusters of high effect size (Cox, 2018).

The following contrasts were computed: 1) canonical sentences in silence > null; 2) canonical sentences in multi-speakers > null; 3) noncanonical sentences in silence > null; 4) noncanonical sentences in multi-speakers > null; 5) the main effect of sentence structure, computed as noncanonical sentences > canonical sentences (across both levels of background noise), and 6) the main effect of masking, computed as sentences in multi-speakers > sentences in silence (across both levels of sentence structure). Follow-up simple comparisons were performed to further explore significant main effects of: 1) sentence structure by contrasting noncanonical sentences to canonical sentences, in silence and in multi-speakers separately; and 2) masking by contrasting sentences in multi-speakers to sentences in silence, in canonical and noncanonical structures separately.

To explore how activation in response to sentence comprehension may differ with hearing loss, AFNI's 3dttest++ with the -covariates option was used to regress participant hearing ability to activation across all voxels in a contrast. Contrasts of interest with this covariate were each sentence condition > null, the main effect of sentence structure, computed as noncanonical sentences > canonical sentences (across both levels of background noise), and the main effect of masking, computed as sentences in multi-speakers > sentences in silence (across both levels of sentence structure). To determine how activation during sentence comprehension is modulated by cognition, contrasts of the main effect of sentence structure and background noise were also correlated with behavioral measures of complex working memory (OST) and attentional control (Simon Task), obtained in each participant in Experiment 2.

A region of interest (ROI) analysis was used to determine if activations in regions identified by contrasts of interest were predictive of sentence comprehension abilities (as measured by RT difference scores from the sentence-picture matching task performed outside the MRI scanner, see Table 1). ROIs were defined in one of two ways: 1) regions whose activation in response to the effect of sentence structure or the effect of masker significantly correlated with participant hearing abilities, and 2) regions whose activation in response to the effect of sentence structure or the effect of masker significantly correlated with participant working memory or attentional control abilities. The mean beta value across voxels was computed within each ROI. Linear regressions were used to predict participant RT difference scores from each ROI's mean beta value. As in Experiment 2, covariates (age, PTA, and WAIS-IV WMI and PSI) were included in the regression models if identified as significant in bivariate correlations with the RT difference scores (see Experiment 2, Table 4).

Lastly, activation in response to sentence comprehension within regions corresponding to the language, frontoparietal, and cingulo-opercular networks as defined in Experiment 2 (see Table 2 for region names and center of mass coordinates), were also explored. Experiment 2 indicated that the functional connectivity between these networks contribute to comprehension of complex sentence structures and speech in noise, therefore this analysis was performed to characterize the involvement of these regions during online sentence comprehension. These ROIs were not defined by a specific sentence condition contrast, therefore paired-samples t-tests were computed to compare activations between the four sentence conditions to determine if each region is significantly more active in one condition compared to another (Bonferroni multiple comparison corrections were applied (0.05/6=0.008)).

Table 2. Network and ROI names and MNI center of mass coordinates

	X	Y	Z
Language Network			
L Inferior Frontal Gyrus (IFG)	-51	26	2
R Inferior Frontal Gyrus (IFG)	54	28	1
L Posterior Superior Temporal Gyrus (pSTG)	-57	-47	15
R Posterior Superior Temporal Gyrus (pSTG)	59	-42	13
Cingulo-opercular Network			
Anterior Cingulate Cortex (ACC)	0	22	35
L Anterior Insula	-44	13	1
R Anterior Insula	47	14	0
Frontoparietal Network			
L Prefrontal Cortex (PFC)	-43	33	28
R Prefrontal Cortex (PFC)	41	38	30
L Posterior Parietal Cortex (PPC)	-46	-58	49
R Posterior Parietal Cortex (PPC)	52	-52	45

Results

FMRI activation to auditory speech comprehension

As expected, voxel-wise t-tests to identify regions that were more active for each sentence condition compared to null trials all identified a similar overall pattern of activation throughout bilateral temporal and inferior parietal cortex, as well as several areas within left frontal cortex.

For example, canonical sentences presented in silence compared to null trials revealed significant activations in bilateral superior and middle temporal gyri (STG and MTG, respectively), extending the length of the temporal lobe to include anterior and posterior temporal regions. (Figure 1, Table 3). Increased activation also was observed in the inferior frontal gyrus (IFG; BA 44 and 45, i.e. Broca’s area), middle frontal and pre-central gyri, and the left medial frontal gyrus (i.e. supplementary motor area). Regions of decreased activation in response to sentences include anterior medial frontal gyrus, posterior cingulate cortex, right posterior middle temporal gyrus and inferior parietal lobule. These regions highly overlap with the well-characterized default mode network whose activity is downregulated in the presence of external stimuli or an explicit task (Fox & Raichle, 2007). Noncanonical sentences presented in silence compared to null trials exhibited a similar pattern of activation (Figure 1, Table 3), including extensive activation within bilateral STG/MTG, left Broca's area, and bilateral precentral gyri. Areas of decreased activation include regions within the default mode network (medial frontal and posterior cingulate) as well as extensive bilateral posterior temporal regions that extend into middle occipital and lingual gyri.

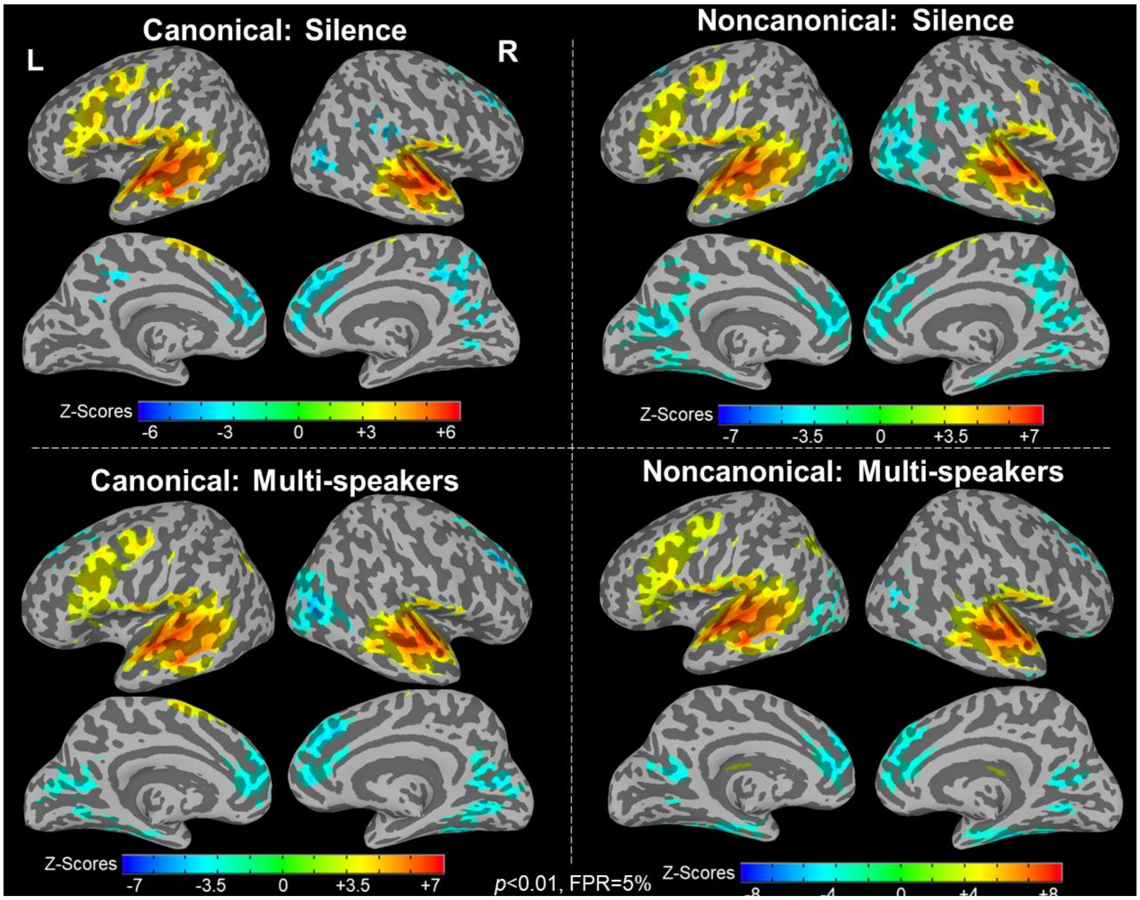

Figure 1. Activation differences to comprehension of sentence condition versus null trials. Areas in warmer colors reflect greater activation for sentences in silence compared to null trials. Areas in cooler colors reflect increased activation for null trials compared to sentences. Voxel-wise threshold *p*<0.01 with a FPR=5%.

Table 3. Significant regions and peak coordinates for the contrast comparing canonical and noncanonical sentences to null trials. (*p*<0.01, FPR=5%)

Region	Peak Coordinates			Cluster Size	Z-Score
Canonical: Silence > Null	X	Y	Z		
L Superior Temporal Gyrus	-63	-15	4	7445	6.80
R Superior Temporal Gyrus	59	-11	6	3356	6.76
L Medial Frontal Gyrus	-5	-1	58	697	4.81
L Precentral Gyrus	-41	-11	32	7	2.83
Null > Canonical: Silence					
L Medial Frontal Gyrus	-3	41	22	2935	-4.86
R Posterior Cingulate Gyrus	5	-39	38	1326	-4.49

R Middle Temporal Gyrus	47	-67	14	273	-4.57
R Inferior Parietal Lobule	55	-35	30	221	-4.68
R Medial Frontal Gyrus	23	3	52	146	-3.14
R Lingual Gyrus	21	-53	0	19	-3.22
R Middle Frontal Gyrus	25	21	56	8	-3.07
Noncanonical: Silence > Null	X	Y	Z		
L Superior Temporal Gyrus	-63	-17	4	8646	7.42
R Superior Temporal Gyrus	57	-11	6	3469	7.60
L Medial Frontal Gyrus	-5	-3	62	1164	4.96
R Precentral Gyrus	55	-11	42	213	4.58
Null > Noncanonical: Silence					
R Middle Temporal Gyrus	41	-73	20	11340	-4.91
R Superior Frontal Gyrus	3	59	22	3408	-4.70
L Middle Frontal Gyrus	-23	19	44	102	-4.77
R Inferior Temporal Gyrus	53	-5	-24	19	-2.98
R Middle Frontal Gyrus	29	3	62	16	-2.94
R Middle Temporal Gyrus	49	-51	0	12	-2.72
R Inferior Temporal Gyrus	47	-11	-22	8	-2.84
R Lingual Gyrus	25	-65	-2	8	-2.73

Activation in response to canonical sentences presented in multi-speakers compared to null trials showed increased activation within bilateral STG/MTG, left Broca’s area, and left middle frontal gyrus (Figure 1, Table 4). Left precentral gyrus activation was also present, although to a lesser extent than in canonical sentences presented in silence. Increased activation from the left STG also extended into the left angular gyrus. Decreases in activation were observed within regions of the default mode network (medial frontal and posterior cingulate), bilateral cuneus, bilateral lingual gyrus, and right posterior middle temporal and middle occipital gyri. Noncanonical sentences presented in multi-speakers compared to null trials also identified increased activation within bilateral STG/MTG extending into left angular gyrus, left Broca’s area, middle frontal gyrus, and precentral gyrus (Figure 1, Table 4). Areas of decreased activation fell mostly within default mode network regions, including the medial temporal lobe.

Table 4. Significant regions and peak coordinates comparing canonical and noncanonical sentences in multi-speakers to null trials. (*p*<0.01, FPR=5%)

Region	Peak Coordinates			Cluster Size	Z-Score
Canonical: Multi-speakers > Null	X	Y	Z		
L Superior Temporal Gyrus	-63	-15	4	7213	7.56
R Superior Temporal Gyrus	51	-11	0	3758	7.10
L Medial Frontal Gyrus	-7	-1	60	672	4.95
L Angular Gyrus	-33	-59	32	194	4.40
R Insula	29	-35	28	5	2.74
Null > Canonical: Multi-speakers					
R Middle Temporal Gyrus	43	-63	10	4362	-5.60

R Middle Frontal Gyrus	27	23	44	3515	-6.17
L Superior Frontal Gyrus	-13	45	44	452	-4.67
L Cuneus	-1	-87	6	17	-3.15
Noncanonical: Multi-speakers > Null	X	Y	Z		
L Superior Temporal Gyrus	-63	-15	4	9476	7.86
R Superior Temporal Gyrus	59	-11	6	4663	7.43
R Insula	29	-9	22	16	2.93
Null > Noncanonical: Multi-speakers					
R Superior Frontal Gyrus	23	39	42	3714	-5.09
R Fusiform Gyrus	27	-25	-20	3704	-5.28
L Posterior Cingulate Gyrus	-17	-57	10	907	-4.57
R Middle Temporal Gyrus	55	-1	-26	327	-4.53
R Inferior Frontal Gyrus (BA 47)	45	27	-10	256	-3.82
R Middle Temporal Gyrus	41	-71	18	133	-4.54
R Middle Temporal Gyrus	43	-61	10	57	-4.80
L Cerebellum	-35	-39	-38	51	-3.67
R Superior Frontal Gyrus	9	25	60	20	-2.90

FMRI results: Effect of sentence structure

The contrast exploring the main effect of sentence structure (noncanonical sentence structures versus canonical sentence structures, collapsed across both levels of background noise) did not reveal any regions of activation that survived multiple comparison corrections. As detailed in the discussion, even though there is a large behavioral effect (see Experiment 2), it is likely that this study was underpowered to detect the effect of sentence structure. The increased processing known to be required by syntactic movement (i.e. the type of sentence structure complexity employed in this study), is known to occur at specific timepoints within a sentence (Hagoort, Brown, & Groothusen, 1993; Kaan, Harris, Gibson, & Holcomb, 2000) and thus the sparse sampling protocol is not ideal to capture this effect while still sampling multiple points within the hemodynamic response across trials in a given condition. Since the main effect of sentence structure was not significant, simple comparisons of activation were not performed.

FMRI results: Effect of masking

To investigate the brain regions involved in comprehension of speech in the presence of multiple, competing speakers, the contrast of sentences in multi-speakers versus sentences in silence, averaged across both levels of sentence structure, was computed (Figure 2, Table 5). This contrast identified increased activations largely within bilateral STG, extending inferiorly into the MTG. Activation in the right temporal lobe extended more posteriorly in the STG than in the left hemisphere. Regions within bilateral parietal lobes also were identified by this masking effect contrast, including the right inferior parietal lobule, right supramarginal gyrus, and the left inferior parietal lobule, as well as midline parietal structures including bilateral posterior cingulate cortex and precuneus.

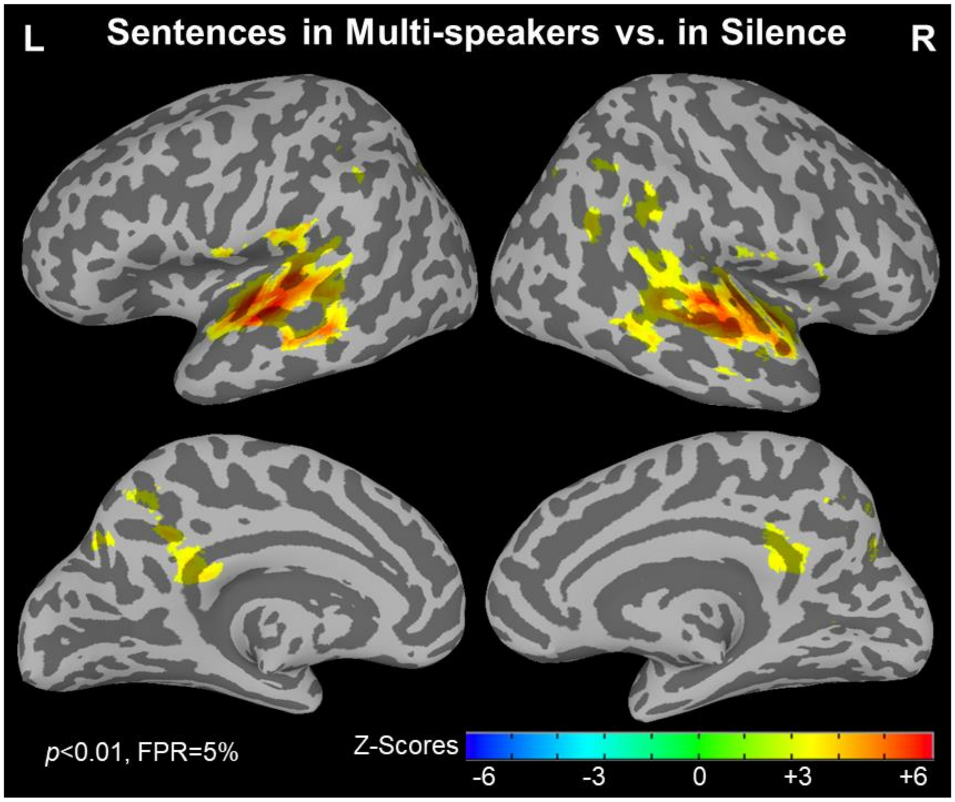

Figure 2. Activation differences to comprehension of sentences in multi-speakers versus sentences in silence collapsed across sentence structures. Areas in warmer colors reflect greater activation for sentences in multi-speakers. Voxel-wise threshold *p*<0.01 with a FPR=5%.

Table 5. Significant regions and peak coordinates for sentences in multi-speakers compared to sentences in silence collapsed across sentence structure. (*p*<0.05, FPR=5%)

Region	Peak Coordinates			Cluster Size	Z-Score
	X	Y	Z		
Multi-speakers > Silence					
R Superior Temporal Gyrus	63	-25	4	3917	6.18
L Superior Temporal Gyrus	-55	-13	2	3137	6.55
L Inferior Parietal Lobule	-41	-33	28	74	3.35
R Anterior Insula	41	9	-2	10	2.74
R Precuneus	31	-65	34	6	2.70
L Posterior Cingulate	-9	-33	32	3	2.69
L Middle Temporal Gyrus	-61	-49	0	2	2.63

R Posterior Cingulate	17	-47	28	2	2.70

A pairwise comparison of speech in multi-speakers to silence within canonical sentence structures revealed activation only within bilateral STG and MTG (Figure 3, Table 6). The same contrast but within noncanonical sentence structures showed prominent activation within bilateral STG and MTG as well, in addition to several other regions: right posterior STG, bilateral inferior parietal lobule, right supramarginal gyrus, bilateral posterior cingulate cortex, bilateral middle occipital gyri extending into the lingual gyri, and the left cuneus (Figure 3, Table 7).

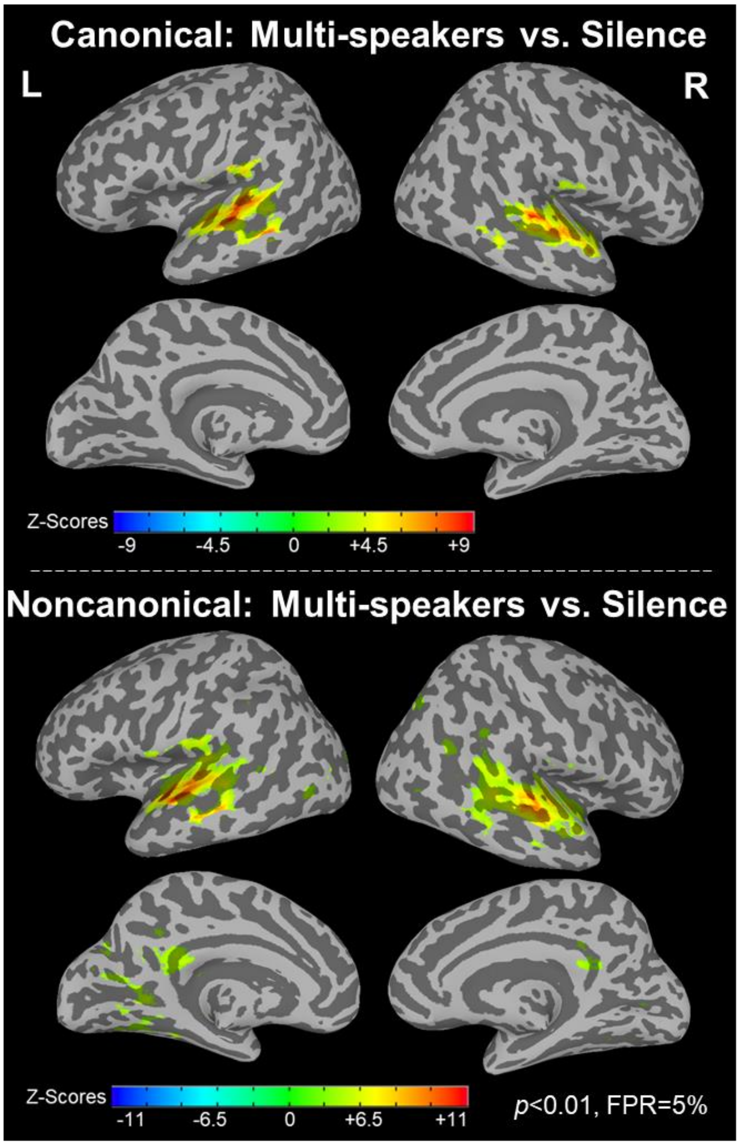

Figure 3. Activation differences to comprehension of canonical and noncanonical sentences in multi-speakers versus silence. Areas in warmer colors reflect greater activation for sentences in multi-speakers. Voxel-wise threshold *p*<0.01 with a FPR=5%.

Table 6. Significant regions and peak coordinates for canonical and noncanonical sentences in multi-speakers compared sentences in silence. (*p*<0.05, FPR=5%)

Region	Peak Coordinates			Cluster Size	Z-Score
	X	Y	Z		
Canonical: Multi-speakers > Silence					
L Superior Temporal Gyrus	-53	-19	6	1583	9.36
R Superior Temporal Gyrus	63	-29	4	1578	9.01
Noncanonical: Multi-speakers > Silence					
L Superior Temporal Gyrus	-55	-13	2	3857	11.01
R Superior Temporal Gyrus	63	-23	4	3520	10.25
L Cuneus	-11	-67	10	229	4.01

L Cerebellum	-9	-47	-8	123	3.40
L Middle Occipital Gyrus	-15	-85	14	20	2.89
R Cerebellum	1	-67	-14	17	3.00
R Anterior Insula	45	7	-4	6	2.69

FMRI activation differences as a function of hearing loss

Voxel-wise correlations between hearing ability and activations in response to each sentence condition compared to null trials were computed to determine how the brain regions recruited during sentence comprehension are related to hearing loss (Figure 4, Table 7). In all four sentence conditions, increasing hearing loss was significantly correlated with increased activation in the bilateral precentral and middle frontal gyri. Increased activation in response to noncanonical sentences in silence also was significantly correlated with increasing hearing loss in the left insula and right putamen. Increased activation in response to noncanonical sentences in multi-speakers was significantly correlated with increasing hearing loss in left anterior cingulate cortex and the left fusiform gyrus. Decreases in activation with increasing hearing loss in all four sentence conditions were observed in right Heschl's gyrus and bilateral lingual gyrus. For noncanonical sentences in silence, several additional regions exhibited decreasing activation with increasing hearing loss, including bilateral precentral gyrus, bilateral precuneus, left inferior parietal lobule and parahippocampal gyrus. For noncanonical sentences in multi-speakers, one additional region in the left middle temporal gyrus exhibited decreased activation that was significantly correlated with increasing hearing loss.

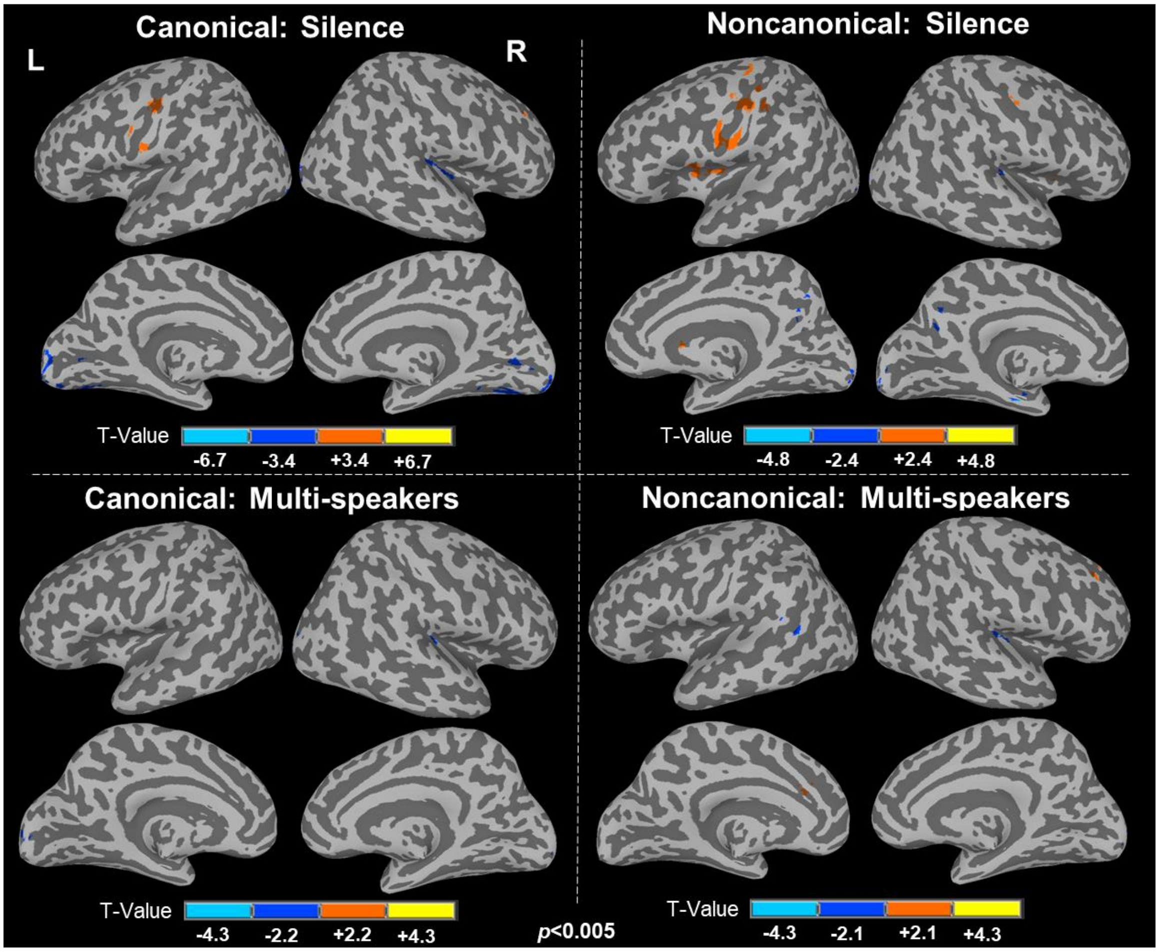

Figure 4. Activation differences to comprehension of sentence condition versus null trials correlated with hearing loss. Areas in orange reflect activation increases with increasing hearing loss. Areas in blue reflect activation decreases with increasing hearing loss. Voxel-wise threshold *p*<0.005.

Table 7. Significant regions and peak coordinates for hearing ability correlated with activation to sentence conditions compared to null trials. (*p*<0.05, FPR=5%, >20 voxels)

Region	Peak Coordinates			Cluster Size	T-Score
	X	Y	Z		
Canonical: Silence					
Positive					
L Precentral Gyrus	-57	-3	22	56	4.34
L Precentral Gyrus	-39	-17	34	51	4.11
R Middle Frontal Gyrus	-27	31	42	33	3.74
Negative					
L Cuneus	-3	-93	0	1093	-6.72
R Heschl’s Gyrus	33	-29	14	189	-4.21
R Lingual Gyrus	-23	-73	2	173	-4.88
L Middle Occipital Gyrus	-15	-87	16	22	-3.84
Noncanonical: Silence					
Positive					
L Insula	-33	7	12	155	4.15
L Precentral Gyrus	-41	-11	28	152	4.61

L Precentral Gyrus	-37	-21	62	28	4.80
Negative					
L Lingual Gyrus	-5	-93	-4	138	-4.34
L Precentral Gyrus	-53	-3	20	119	4.84
R Putamen	23	9	8	80	3.93
R Lingual Gyrus	11	-89	-6	77	-3.99
L Middle Occipital Gyrus	-33	-55	2	46	-3.83
L Precuneus	-9	-63	30	44	-3.89
L Parahippocampal Gyrus	-37	-11	-18	35	-4.13
R Precuneus	15	-53	34	35	-3.74
R Heschl’s Gyrus	29	-29	10	32	-3.94
R Precuneus	3	-57	34	31	-3.50
L Inferior Parietal Lobule	-33	-45	26	30	-3.86
R Precentral Gyrus	43	-19	38	24	3.54
Canonical: Multi-speakers					
Positive					
R Middle Frontal Gyrus	33	37	-10	31	3.72
Negative					
L Cuneus	-13	-95	0	187	-4.34
R Lingual Gyrus	17	-91	-2	86	-4.13
R Heschl’s Gyrus	37	-27	14	22	-3.51
Noncanonical: Multi-speakers					
Positive					
R Middle Frontal Gyrus	23	33	38	52	3.92
L Fusiform Gyrus	-43	-17	-22	22	4.16
L Anterior Cingulate	-7	23	26	23	4.18
Negative					
L Middle Temporal Gyrus	-59	-47	8	67	-4.23
R Heschl’s Gyrus	33	-25	12	43	-4.25
L Lingual Gyrus	-25	-65	-2	40	-3.76

Correlations also were computed between hearing abilities and activation differences across conditions that represent the effects of sentence structure and masker. These analyses were conducted to examine how hearing modulates the brain regions specifically involved with comprehending complex sentence structures and sentences in noise.

Effect of sentence structure and hearing loss: Increased activation for noncanonical sentences compared to canonical sentences correlated with increasing hearing loss in the middle segment of the right middle temporal gyrus, left cuneus, and left anterior cingulate cortex (Figure 5, Table 8). Decreased activation for noncanonical sentences compared to canonical sentences correlated with increasing hearing loss in several regions including bilateral parahippocampal gyri, left inferior medial frontal gyrus, and the right anterior middle temporal gyrus. Out of all these regions, the RT effect of sentence structure (from experiment 2’s behavioral sentence comprehension task) was only significantly predicted by activation within the left cuneus region identified (*r*=.449, *p*=0.19), such that poorer comprehension abilities for sentences with noncanonical structures were associated with increased activation in this region.

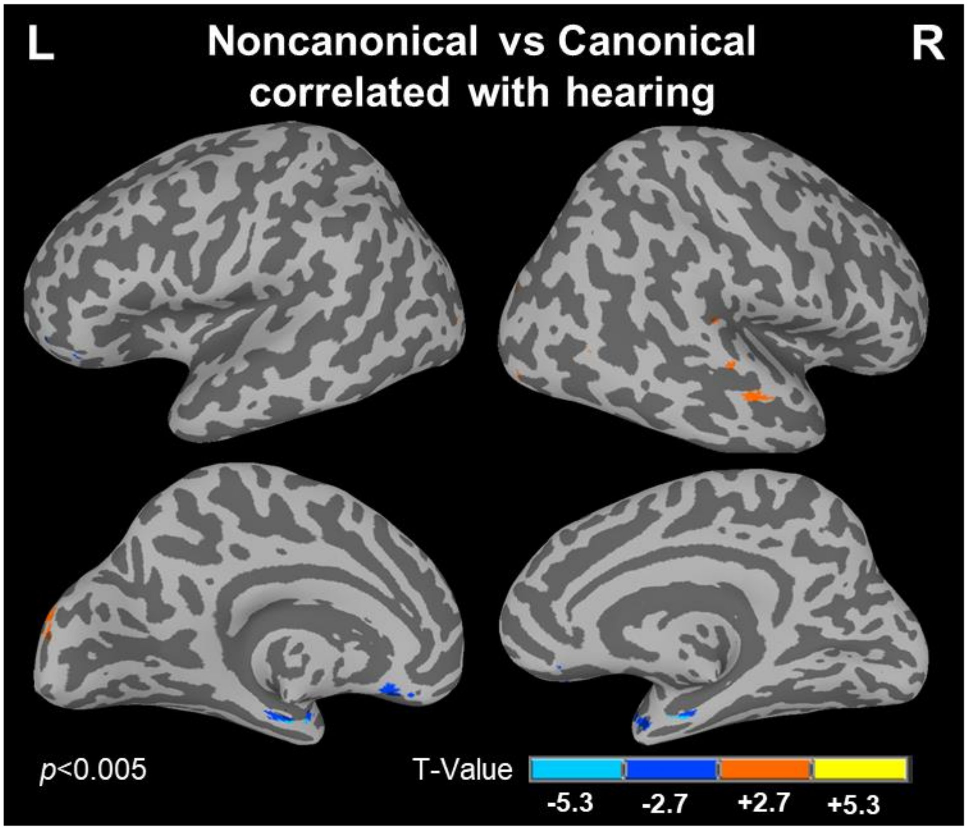

Figure 5. Activation differences to comprehension of noncanonical versus canonical sentences correlated with hearing loss. Areas in orange reflect activation increases with increasing hearing loss. Areas in blue reflect activation decreases with increasing hearing loss. Voxel-wise threshold *p*<0.005.

Table 8. Significant regions and peak coordinates for activation to noncanonical sentences compared to canonical sentences correlated with hearing abilities. (*p*<0.005, clusters > 20 voxels)

Region	Peak Coordinates			Cluster Size	T-Value
Positive correlations	X	Y	Z		
R Middle Temporal Gyrus	55	-27	2	53	4.18
R Cuneus	3	-95	12	49	4.35
L Cuneus	-11	-95	12	29	4.38
Negative correlations					
L Parahippocampal Gyrus	-13	-7	-20	343	-4.80
R Parahippocampal Gyrus	17	-7	-16	114	-4.27
R Superior Temporal Gyrus	29	11	-24	74	-5.07
L Medial Frontal Gyrus	-11	27	-16	44	-4.05

Effect of masker and hearing loss: Increased activation for sentences in the multi-speaker masker compared to in silence that correlated with increasing hearing loss was identified in portions of bilateral superior frontal and medial frontal gyri, right middle frontal gyrus, bilateral middle and inferior temporal gyri, and anterior cingulate (Figure 6, Table 9). Regions exhibiting a correlation between decreased activation in response to the masker and increasing hearing loss included portions of the bilateral precentral and postcentral gyri, right inferior frontal gyrus (overlapping with BA 45) and insula, right inferior parietal lobule, and right supramarginal gyrus. Activation in these regions did not significantly predict the related behavioral measures of sentence comprehension (i.e. RT effect of maskers).

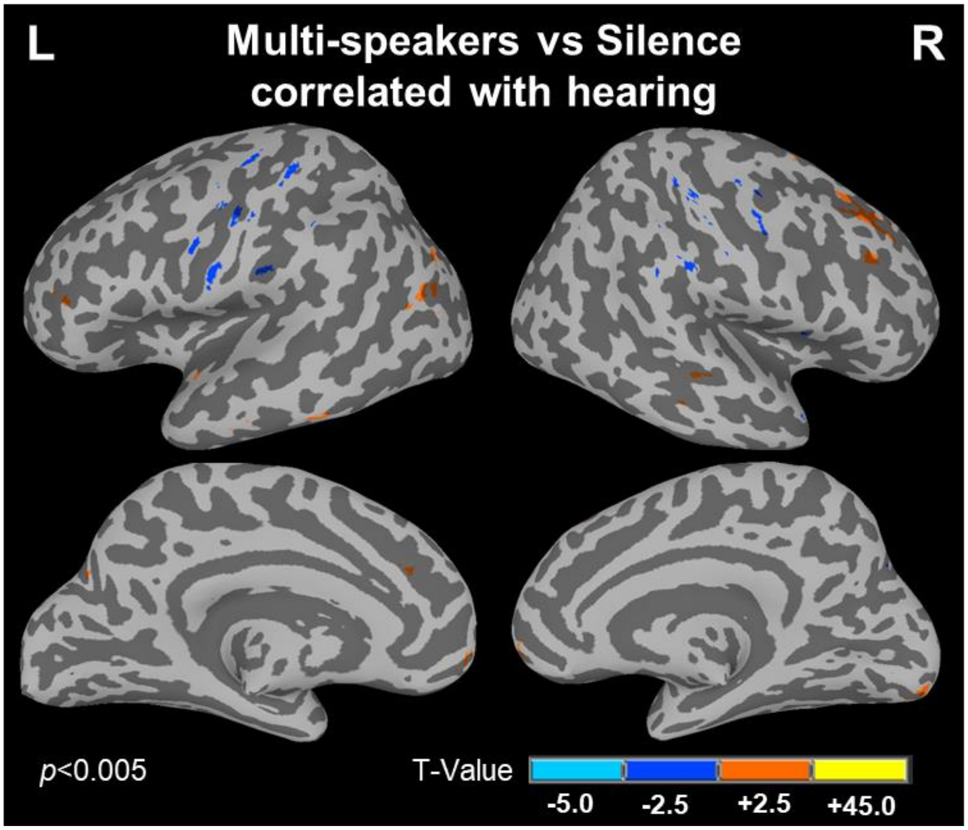

Figure 6. Activation differences to comprehension of sentences in multi-speakers versus sentences in silence correlated with hearing loss. Areas in orange reflect activation increases with increasing hearing loss. Areas in blue reflect activation decreases with increasing hearing loss. Voxel-wise threshold $p<0.005$.

Table 9. Significant regions and peak coordinates for activation to sentences in multi-speakers compared to sentences in silence correlated with hearing abilities. (*p*<0.005, clusters > 20 voxels)

Region	Peak Coordinates			Cluster Size	T-Value
Positive correlations	X	Y	Z		
R Middle Frontal Gyrus	29	19	30	200	4.52
R Medial Frontal Gyrus	13	37	40	91	4.56
R Inferior Temporal Gyrus	67	-29	-20	67	4.60
L Inferior Temporal Gyrus	-59	-21	-16	60	4.39
L Superior Frontal Gyrus	-7	37	44	38	4.06
L Anterior Cingulate	-5	53	-2	36	4.39
L Cuneus	-27	-79	28	30	4.49
R Parahippocampal Gyrus	33	-51	-4	27	4.41
L Middle Temporal Gyrus	-35	-65	22	27	4.24
L Middle Temporal Gyrus	-45	-67	16	24	3.91
L Medial Frontal Gyrus	-13	49	-4	21	4.24
Negative correlations					
L Postcentral Gyrus	-43	-15	54	68	-4.23
L Precentral Gyrus	-55	-3	20	57	-4.31
R Postcentral Gyrus	63	-23	34	51	-3.83
R Precentral Gyrus	39	-17	42	43	-5.00
L Postcentral Gyrus	-49	-17	18	26	-4.09
R Inferior Frontal Gyrus	47	15	20	25	-4.01
R Postcentral Gyrus	47	-29	54	21	-3.51

FMRI activations during sentence comprehension as a function of cognition

Sentence structure effect and cognition: Correlations between working memory and attentional control abilities (as measured by the OST and Simon Task, respectively, see Experiment 2) and activations reflecting the effect of sentence structure and masking were conducted to determine if the brain regions involved in challenging sentence comprehension differed with individual cognitive abilities. Increased activation in the left posterior middle temporal gyrus in response to the effect of sentence structure was found to be significantly correlated with better working memory performance (Figure 7, Table 10). Lower working memory performance was associated with increased activation in right inferior frontal and inferior temporal gyri in response to sentence structure. Poorer attentional control performance correlated with increased activation in response to the sentence structure effect in the right posterior superior temporal gyrus, right inferior frontal gyrus, and the anterior cingulate (Figure 8, Table 11). Better attentional control was not significantly correlated with increased activations to sentence structure in any regions. Activation in the regions identified by the correlations did not significantly predict the RT behavioral effect of sentence structure.

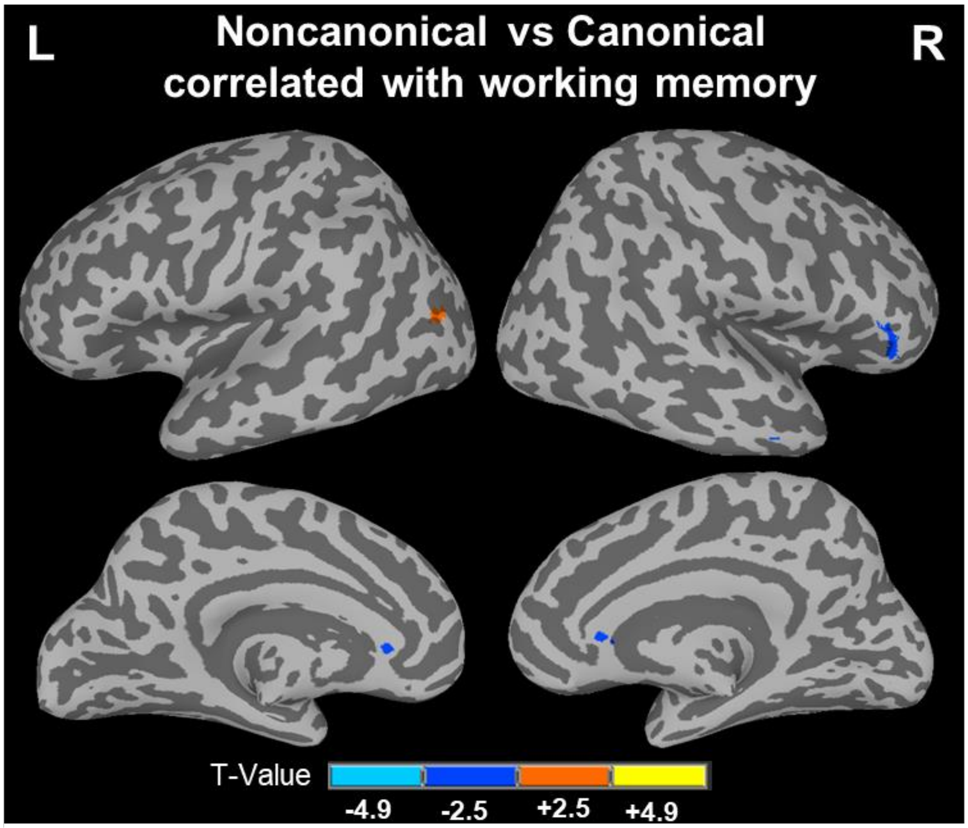

Figure 7. Activation differences to comprehension of noncanonical versus canonical sentences correlated with working memory. Areas in orange reflect activation increases with better working memory. Areas in blue reflect activation increases with poorer working memory. Voxel-wise threshold *p*<0.005.

Table 10. Significant regions and peak coordinates for activation to noncanonical compared to canonical sentences correlated with working memory. (*p*<0.005, clusters > 20 voxels)

Region	Peak Coordinates			Cluster Size	T-Value
Positive correlations	X	Y	Z		
L Middle Temporal Gyrus	-35	-63	14	63	4.06
Negative correlations					
R Inferior Frontal Gyrus	53	29	0	82	-4.91
R Inferior Temporal Gyrus	65	-7	-18	23	-4.69

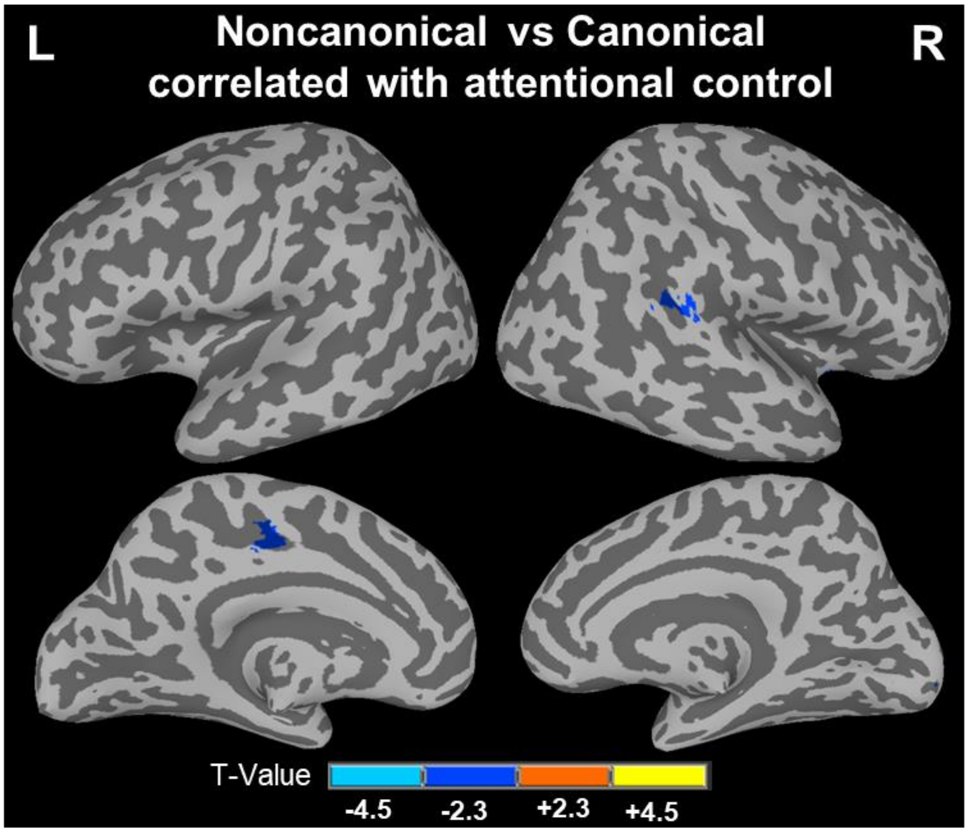

Figure 8. Activation differences to comprehension of noncanonical versus canonical sentences correlated with attentional control. Areas in orange reflect activation increases with better attentional control. Areas in blue reflect activation increases with poorer attentional control. Voxel-wise threshold *p*<0.005.

Table 11. Significant regions and peak coordinates for activation to noncanonical compared to canonical sentences correlated with attentional control. (*p*<0.005, clusters > 20 voxels)

Region	Peak Coordinates			Cluster Size	T-Value
Negative correlations					
R Posterior Superior Temporal Gyrus	65	-43	20	82	-4.50
L Anterior Cingulate Cortex	-11	-17	42	81	-3.76
R Anterior Cingulate Cortex	17	-21	42	34	-3.98
R Inferior Frontal Gyrus	37	11	-12	20	-3.60

Masking effect and cognition: Better working memory performance was associated with increased activation for the effect of masker within the left superior frontal gyrus and right cuneus. Poorer working memory correlated with increased activation within several regions: bilateral precentral, middle frontal, and supramarginal gyri, bilateral precuneus, right inferior and superior frontal gyri, left superior parietal lobule, and the anterior and posterior cingulate (Figure 9, Table

12). Increased activations within the right middle temporal gyrus and the posterior cingulate were associated with better attentional control performance (Figure 10, Table 13). Poorer attentional control performance correlated with increased activation in bilateral precentral gyrus and precuneus, right medial frontal gyrus (near the dorsal anterior cingulate), and the right insula. Activations in these regions did not significantly predict the behavioral RT effect of masker.

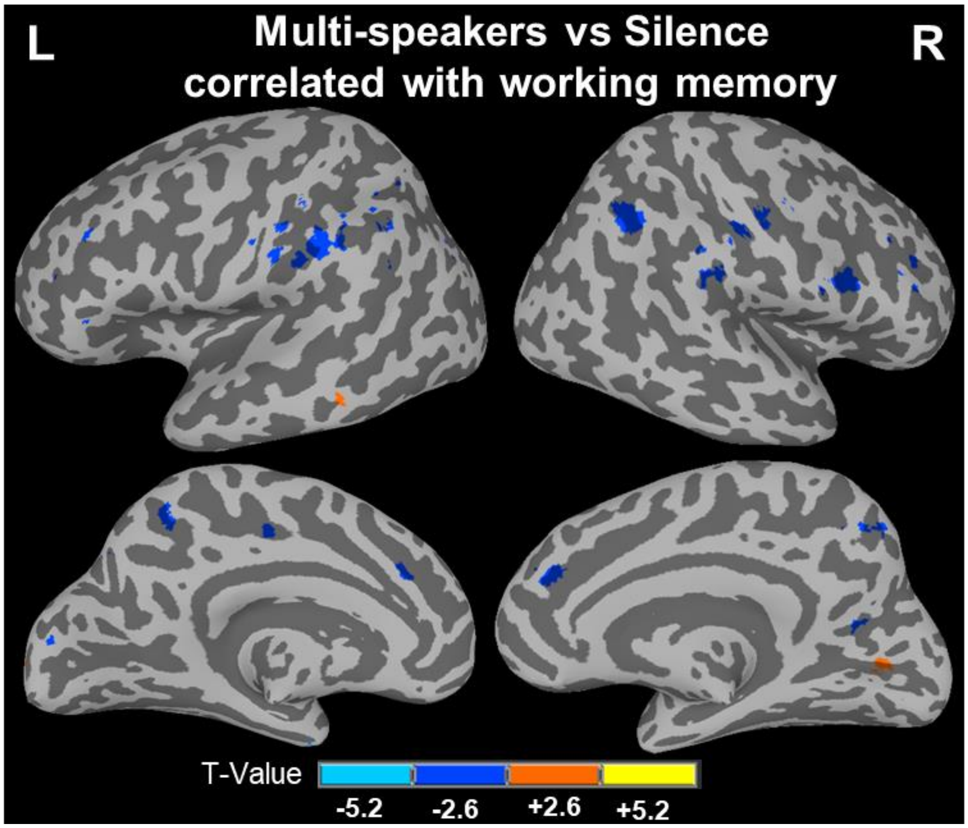

Figure 9. Activation differences to comprehension of sentences in multi-speakers versus sentences in silence correlated with working memory. Areas in orange reflect activation increases with better working memory. Areas in blue reflect activation increases with poorer working memory. Voxel-wise threshold *p*<0.005.

Table 12. Significant regions and peak coordinates for activation to sentences in multi-speakers compared to silence correlated with working memory. (*p*<0.005, clusters > 20 voxels)

Region	Peak Coordinates			Cluster Size	T-Value
Positive correlations	X	Y	Z		
L Superior Frontal Gyrus	-11	55	-2	29	4.39
R Cuneus	19	-71	6	22	4.02
Negative correlations					
L Postcentral Gyrus	-45	-23	34	181	-4.31
R Inferior Frontal Gyrus	39	3	20	151	4.61
R Superior Frontal Gyrus	23	61	12	109	-4.36

R Angular Gyrus	41	-44	34	99	-5.24
R Supramarginal Gyrus	55	-37	30	71	-3.98
R Postcentral Gyrus	49	-21	38	68	-4.40
R Anterior Cingulate Cortex	11	37	20	60	-4.42
L Precuneus	-9	-51	46	42	-3.81
L Supramarginal Gyrus	-43	-47	32	40	-3.61
R Posterior Cingulate Cortex	13	-53	20	33	-3.42
R Middle Frontal Gyrus	31	31	26	32	-3.63
R Precuneus	9	-55	46	32	-4.04
R Middle Frontal Gyrus	45	27	28	26	-3.68
L Middle Frontal Gyrus	-45	29	28	23	-4.07
L Superior Parietal Lobule	-31	-51	48	21	-3.76

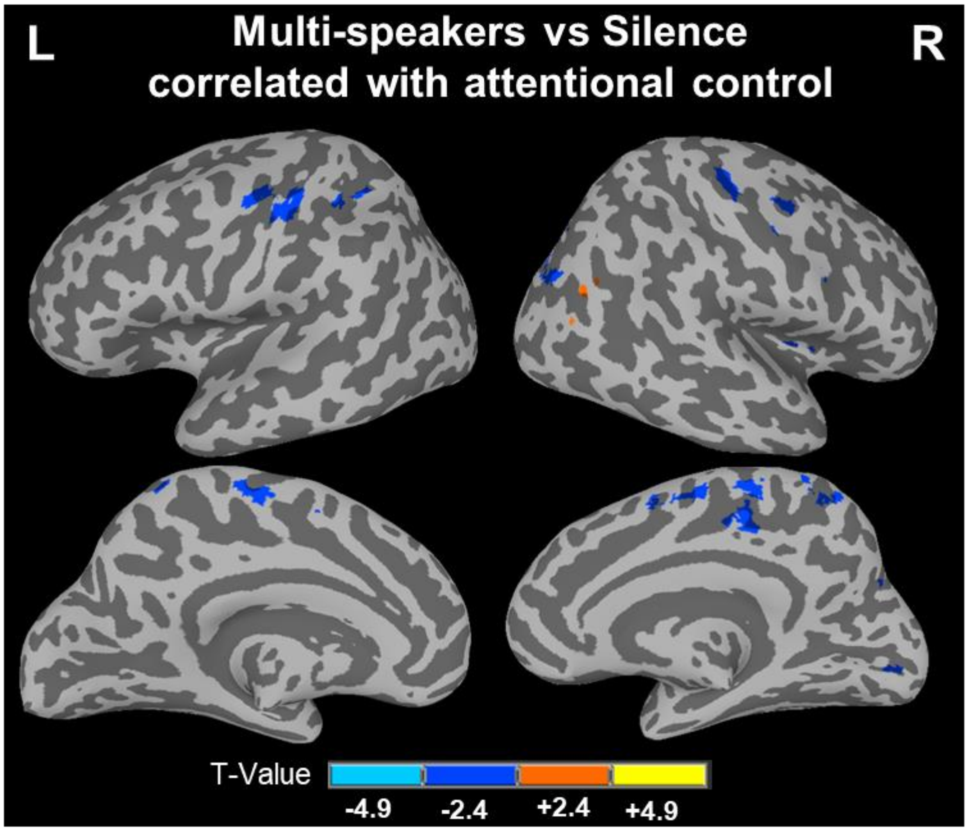

Figure 10. Activation differences to comprehension of sentences in multi-speakers versus sentences in silence correlated with attentional control. Areas in orange reflect activation increases with better attentional control. Areas in blue reflect activation increases with poorer attentional control. Voxel-wise threshold *p*<0.005.

Table 13. Significant regions and peak coordinates for activation to sentences in multi-speakers compared to silence correlated with attentional control. (*p*<0.005, clusters > 20 voxels)

Region	Peak Coordinates			Cluster Size	T-Value
Positive correlations	X	Y	Z		
R Middle Temporal Gyrus	43	-65	22	48	4.85
R Posterior Cingulate Cortex	19	-47	22	38	4.13

Negative correlations					
R Medial Frontal Gyrus	1	-5	50	340	-4.90
L Precentral Gyrus	-43	-15	44	117	-4.83
L Precuneus	-1	-53	62	99	-3.91
R Precentral Gyrus	43	-13	40	54	-4.43
R Precuneus	27	-77	22	46	-3.79
R Lingual Gyrus	11	-81	2	44	-3.85
L Inferior Parietal Lobule	-31	-41	42	44	-3.50
R Postcentral Gyrus	31	-29	46	37	-3.73
R Insula	37	-5	8	36	-4.23
R Precuneus	21	-65	34	23	-4.13
R Precentral Gyrus	47	-3	30	22	-4.29

Network ROI analysis

ROIs from the network analysis described in Experiment 2 corresponding to the language network (bilateral IFG and posterior STG), the frontoparietal network (bilateral prefrontal cortex and posterior inferior parietal cortex), and the cingulo-opercular network (dorsal anterior cingulate and bilateral anterior insula) were used to determine if activation within each of these network ROIs significantly differed in each sentence condition. Paired-samples t-tests indicate that the right posterior STG exhibited increased activation in response to noncanonical sentences in multi-speakers compared to noncanonical sentences in silence (t=3.84, p<0.001; Figure 11) and compared to canonical sentences in silence (t=3.30, p=0.001). This right pSTG region also elicited greater activation in canonical sentences in multi-speakers compared to noncanonical sentences in silence (t=2.89, p=0.004). The right anterior insula also exhibited greater activation for noncanonical sentences in multi-speakers than for canonical sentences in silence (t=2.57, p=0.008; Figure 11).

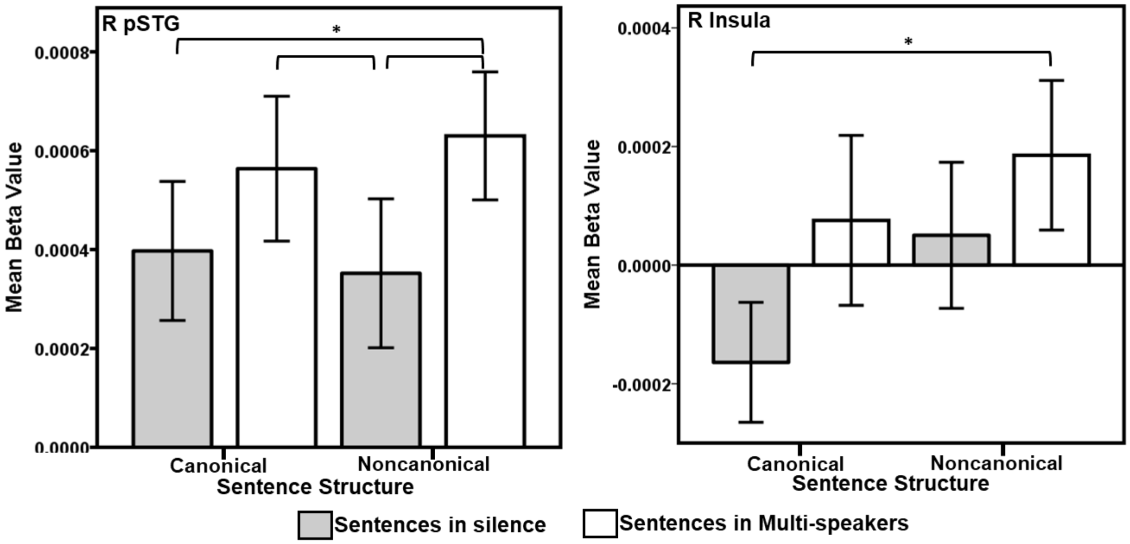

Figure 11. Right: Mean beta value from the R pSTG ROI of the language network from each sentence condition. Left: Mean beta value from the R anterior insula ROI of the cingulo-opercular network from each sentence condition. Bars are grouped by the level of sentence structure. Bar color indicates level of background noise. Gray=silence, white=multi-speakers. Bars reflect one SEM. * indicates *p*<0.008.

The behavioral RT effect of informational masking was significantly predicted by regions within the frontoparietal and language networks: activation within the left lateral prefrontal ROI of the frontoparietal network significantly predicted the behavioral masker effect (ß = .454, *p* = 0.009), even after controlling for the significant covariate (Processing Speed: ß = -.401, *p* = 0.019). Activation within the left IFG of the language network also significantly predicted the effect of masker (ß = .529, *p* = 0.002) after accounting for the significant covariate (Processing Speed: ß = -.553, *p* = 0.001). However, activations within the network ROIs did not significantly predict the behavioral RT effect of sentence structure or the RT effects of the interaction of masker and sentence structure.

Discussion

The aims of this experiment were (i) to identify the brain regions recruited during challenging auditory sentence comprehension in older adults, (ii) examine how recruitment is modified by hearing loss and cognition, and (iii) determine how these activations may be related to sentence comprehension abilities. This experiment was designed to complement Experiment 2 by further characterizing the cognitive and neurobiological resources that support auditory speech comprehension in older adults using a different methodology (task-based fMRI versus resting-state fMRI). The findings indicate that, in response to sentence difficulty (either due to sentence structure or masking), older adults largely engage brain regions within the bilateral fronto-temporo-parietal network that is classically ascribed to language comprehension, but that the recruitment of regions outside of this network are modulated by an individual's hearing, working memory, and attentional control abilities.

Functional resources supporting comprehension of sentences in background noise

The fMRI activation analysis of the effect of masker (sentences in multi-speakers versus sentences in silence) revealed that speech in multi-speaker background noise recruits bilateral superior and middle temporal gyri to a greater degree than sentences presented alone. This contrast also identified increased activation in regions of right angular and supramarginal gyri and bilateral inferior parietal and precuneus regions. Simple comparisons revealed that the increased activation observed within these parietal regions is driven by activation in response to the most difficult sentence condition, the interaction of noncanonical sentences in multi-speakers. This increased activation within the inferior parietal lobe in response to speech in multi-speakers falls near the posterior parietal regions of the frontoparietal network.

The analysis of the network ROIs identified in Experiment 2 revealed that the right posterior superior temporal gyrus of the language network is more activated by speech in multi-speaker backgrounds compared to speech in silence. Further, increased activation within ROIs of the frontoparietal (left prefrontal cortex ROI) and language (left inferior frontal gyrus ROI) networks were also related to comprehension abilities, such that increased activation within these regions was associated with poorer comprehension of speech within informational masking. In Experiment 2, it was reported that increased functional connectivity between the language and frontoparietal networks significantly predicted older adults' improved comprehension of speech in background noise (specifically, informational masking). Together, the data from these two experiments suggest that both functional activation and functional connectivity of the language and frontoparietal networks are involved in the comprehension of speech in background noise, perhaps particularly driven by informational masking. But critically, the findings also suggest that increased functional connectivity between these networks is related to better comprehension abilities of speech in multi-speaker environments but increased activation within the networks while listening to and comprehending speech does not correlate with better comprehension.

Hearing loss also impacts the brain regions recruited in response to speech in noise. The activation effect of masker revealed increased activation in right middle frontal gyrus associated with increasing hearing loss, further supporting the role of the frontoparietal network in speech in noise comprehension as outlined in Experiment 2. The effect of masker additionally revealed that decreased activation within bilateral pre- and postcentral gyri was associated with increasing hearing loss. However, increased activation in left precentral gyrus correlated with increased hearing loss for sentences in silence versus null but not for sentences in multi-speakers. Some neuroanatomical models of auditory speech processing include primary sensorimotor cortex and posit that these regions are involved in auditory-motor integration, contributing to the mapping the articulatory representations of speech sounds (Rauschecker and Scott, 2009; Wilson et al., 2004). Thus, these results may suggest that older adults with a hearing loss activate sensorimotor cortex to a greater degree in response to speech in quiet environments but have diminished access to sensorimotor cortex during the comprehension of speech in multi-speaker environments.

Working memory and cognitive control abilities also are correlated with differential activation patterns in response to the effect of masker. Poorer working memory abilities were associated with increased activation within a large region of the right angular gyrus, again implicating the involvement of the frontoparietal network and working memory in speech comprehension in multi-speaker backgrounds. Results from Experiment 2 indicate that poorer complex working memory performance was associated with poorer comprehension in energetic masking. The results of the present experiment suggest that individuals with poorer working memory may recruit regions within the frontoparietal network in response to speech in noisy environments. Conversely, poorer attentional control revealed increased activation largely within the dorsal anterior cingulate of the cingulo-opercular network, as well as the right insula. This finding supports the relationship between behavioral attentional control performance and functional connectivity within the cingulo-opercular network as reported in Experiment 2. Results from Experiment 2 further link functional connectivity within the cingulo-opercular network to comprehension of complex sentence structures. Together, these findings reveal that, in individuals with poorer attentional control, the cingulo-opercular network is recruited in response to speech in multi-speaker backgrounds and that functional connectivity within this network is related to comprehending complex sentence structures.

Functional resources supporting comprehension of sentences with complex structure

The analyses reported do not provide an adequate general characterization of the brain regions supporting comprehension of complex sentence structures, as the contrast of the effect of sentence structure (noncanonical sentences greater than canonical sentences) did not reveal any voxels which survived multiple comparison corrections. These nonsignificant findings were likely due to this effect being underpowered. The sparse design of the fMRI paradigm resulted in only 20 stimuli per condition and only three timepoints (i.e. MR images) per stimuli. While the presence of background noise persisted throughout the entire sentence presentation, there is a much smaller timeframe in which the complexity of the noncanonical sentences manifests (approximately the last half of the sentence). However, the analyses correlating the activation effect of sentence structure with individual hearing and cognitive abilities do reveal distinct brain regions supporting comprehension.

Similar to one previous study of sentence comprehension (Peelle et al., 2011), hearing loss was associated with decreased activation within right Heschl’s gyrus across all sentence conditions. Increasing hearing loss was also associated with increased activation to noncanonical sentences in silence within the left insula and to the interactive effect of noncanonical sentences in multi-speakers within the dorsal anterior cingulate. These findings mirror results from Experiment 1 wherein functional connectivity between right Heschl’s gyrus and regions of the cingulo-opercular network (i.e. bilateral insula and dorsal anterior cingulate) increased with increasing hearing loss. It is possible that the decreases in activation in right Heschl’s gyrus in response to speech (or auditory stimuli more generally) may, over time, lead to increased functional connectivity to the cingulo-opercular network as a way to devote more attention resources to the diminished auditory input, which is then reflected in increased activation within this network while comprehending challenging speech.

Across all four sentence conditions, hearing loss was associated with decreased activation within regions of the occipital cortex (e.g. cuneus, lingual, and middle occipital gyri). However, activations in response to sentence structure that correlated with hearing loss included increased activation in the right cuneus. In addition, as activation within this region increased, comprehension for complex sentence structures decreased. Studies using animal models indicate that, in response to auditory stimuli, auditory cortical activation reciprocally inhibits primary visual cortex (Teichert & Bolz, 2018), and there is evidence to suggest that in normal-hearing adults, auditory stimuli can interfere with visual processing (Hidaka & Ide, 2015). However, no study has investigated the interaction between primary auditory and visual cortices in older adults with hearing loss. The present study's findings suggest that individuals with hearing loss may suppress activation in visual cortical regions in response to auditory speech stimuli, but that those who are less efficient in this suppression have poorer comprehension abilities, particularly as it relates to complex sentence structures.

Poorer working memory and attentional control both also correlated with activation increases in response to the effect of sentence structure. Similar to what was observed in the activation effect of masker, poorer attentional control performance was associated with increased activation to the effect of sentence structure within the dorsal anterior cingulate of the cingulo-opercular network. In Experiment 2, increased accuracy for noncanonical sentences was associated with decreased connectivity and poorer attentional control abilities. However, "poorer" attentional control performance may instead reflect a more careful response strategy during the attentional control task. Thus, it is possible that increased activation within the dorsal anterior cingulate reflects the increased demand on attentional control resources in response to comprehending complex sentence structures. Over time, the increased recruitment of the anterior cingulate in the face of increased cognitive demands may result in functional connectivity dysregulation within the cingulo-opercular network, mirroring studies of cingulo-opercular connectivity declines with age (He et al., 2014).

Conclusion

The present study investigated how the brain regions recruited in response to challenging auditory speech comprehension differ with individual hearing, working memory, and attentional control abilities. The results suggest that comprehending speech in multi-speaker environments recruits regions within the frontoparietal network in individuals with hearing loss and poor working memory abilities, and regions within the cingulo-opercular network in individuals with poor attentional control abilities. Comprehending sentences in complex structures recruits regions within the cingulo-opercular network in individuals with hearing loss and poor attentional control abilities. While the recruitment of these regions did not significantly predict sentence comprehension measured outside the MRI scanner, they do provide insights into individual differences in the neuroanatomical mechanisms supporting challenging auditory speech comprehension, particularly as a function of hearing loss and cognitive abilities.

CHAPTER 5

CONCLUSIONS

The purpose of this dissertation was to probe how hearing, cognition, and functional brain networks contribute to challenging auditory speech comprehension in older adults. Experiment 1 used resting-state fMRI to investigate how resting-state functional connectivity between Heschl's gyri and several sensory and cognitive brain networks changes with hearing loss and age. Experiment 2 utilized behavioral and functional connectivity measures reflecting working memory and attentional control abilities to explore how they predict challenging speech comprehension, after controlling for hearing loss. Experiment 3 used a passive-listening fMRI paradigm to identify 1) the brain regions recruited in response to two types of challenging speech comprehension, 2) how the brain's response may differ by hearing and cognitive abilities, and 3) if brain activation is predictive of comprehension abilities. Across these experiments, two aspects of auditory speech were examined to capture the types of challenges often encountered in everyday life: noisy background environments and complex sentence structures. The impact of hearing loss and cognitive abilities on comprehension, and the brain regions supporting comprehension, also were explored.

Comprehension of speech in noisy environments

Collectively the results from Experiments 2 and 3 indicated that working memory and the frontoparietal network were involved in comprehending speech in background noise in older adults. Specifically, the added cognitive demand of comprehending speech in multi-speaker backgrounds (i.e. informational masking) was predicted by both within-network functional connectivity of the frontoparietal network and functional connectivity between the frontoparietal and language networks in Experiment 2. While the contributions of informational versus energetic (i.e. speech in broadband noise) could not be dissociated in Experiment 3, results from that experiment revealed increased activation within regions of the frontoparietal and language networks in response to speech in a multi-speaker background. Specifically, Experiment 3 identified regions in the right posterior temporal and inferior parietal lobes with greater activation in response to speech in multi-speakers compared to speech in silence, and regions within left inferior and middle frontal gyri whose activation significantly predicted comprehension of speech in informational masking. These findings mirror studies of speech comprehension that identify increased activation in regions within the frontoparietal network but in response to sentences with complex structures (Grossman et al., 2002; Peelle et al., 2009; Tyler et al., 2009), not speech in background noise as observed in this study.

Comprehension of speech in energetic masking was predicted by a measure of complex working memory, whereas comprehending speech in informational masking was predicted by a measure of simple working memory. These results suggest that overcoming acoustic degradation of a target speech signal more generally (present in both energetic and informational masking) may rely upon some elements of complex working memory (e.g. shifting of attention, manipulation of information, rehearsal and maintenance of information), but that over and above this challenge, understanding a target speaker from among background speakers may rely specifically upon simple working memory (e.g. rehearsal and maintenance of the target speech signal). These results align with the Ease of Language Understanding model which posits that working memory holds misheard speech (either due to hearing loss or background noise) in memory for further information and processing (Rönnberg et al., 2013). Collectively, these findings illustrate that older adults' ability to understand speech in noisy environments is supported by multiple aspects of working memory and involvement of the frontoparietal and language networks. Thus, the frontoparietal network and the working memory functions it supports may serve as a target for future studies seeking to improve challenging speech comprehension in older adults.

Comprehension of complex sentence structure

Similar to the findings of the resources supporting the comprehension of speech in noisy environments, Experiments 2 and 3 implicate working memory in the comprehension of auditory sentences with complex structures, as commonly reported (Goral et al., 2011; Just & Carpenter, 1992; Norman et al., 1992). These experiments also indicate that comprehending complex sentence structures is related to attentional control and the cingulo-opercular network. Behaviorally, Experiment 2 replicated the well-studied effect that sentences with complex noncanonical structures yield lower comprehension accuracies and longer reaction times than sentences with simpler, canonical structures (Ferreira, 2003; King & Just, 1991; Wilson et al., 2010). But notably, the cognitive and neural resources involved in comprehending complex sentence structures were less robust and often in the opposite direction as expected. For instance, poorer attentional control ability and decreased within-network functional connectivity of the cingulo-opercular network predicted better comprehension of sentences with complex structures. These findings may reflect age-related changes in response strategy in the face of attention-demanding tasks, making typical interpretations of reaction time difference scores commonly used in studies of younger adults difficult to apply to and interpret in cohorts of older adults (Knight & Heinrich, 2017; Starns & Ratcliff, 2010). Age-related changes in task response strategies also may be related to age-related dysregulation within the cingulo-opercular network (He et al., 2014). Thus, it is possible that the processes involved in comprehending complex sentence structures are particularly susceptible to changes in attentional control and in the cingulo-opercular network that occur with age.

Impact of hearing loss on the brain and comprehension

Experiments 1 and 3 probed the impact that hearing loss has upon brain resting-state functional connectivity and activation in response to comprehending challenging auditory speech. Experiment 1 revealed that increased hearing loss was associated with increased functional connectivity between right Heschl's gyrus and all regions within the cingulo-opercular network and the right inferior frontal gyrus of the language network. Similarly, Experiment 3 revealed that activation within right Heschl's gyrus decreased with increasing hearing loss in response to both masking and complex sentence structures. Together these findings suggest that mild to moderate hearing loss in older adults may lead to reduced sensitivity of right Heschl's gyrus to speech, resulting in increased reliance upon connections to the brain networks related to attentional control (i.e. the cingulo-opercular network) and the right hemisphere homologues of the speech comprehension network.

Behaviorally, hearing loss was significantly related to comprehension of speech in energetic masking, but not informational masking. Similar to the relationship between complex working memory and masking, this finding suggests that hearing loss results in poorer comprehension of acoustically degraded speech signals more generally, but not in the additional cognitive demands involved in comprehending the target speaker from among distracting, background speakers. Hearing loss also was associated with poorer comprehension of sentences with complex structures, suggesting that hearing loss may interact with the cognitive abilities that support speech comprehension both in noisy backgrounds and with complex sentence structures.

Final conclusions

In summary, the experiments presented here identify the contributions of hearing loss, working memory, and attentional control, and functional brain resources to challenging auditory speech comprehension in older adults. The findings indicate that working memory abilities and the functionality of the frontoparietal and language networks support the comprehension of speech in multi-speaker environments. Conversely, attentional control and the cingulo-opercular networks are implicated in the comprehension of complex sentence structures. Lastly, hearing loss was shown to influence speech comprehension performance due to energetic masking only, and to impact the activation and functionality connectivity of right Heschl’s gyrus. Together, these findings point to potential cognitive functions or brain networks that may serve as future targets for interventions to improve communication, and therefore quality of life, in older adults.

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APPENDIX A

SUPPLEMENTARY TABLES AND FIGURES

Table 1A. Mean participant performance on cognitive tasks

Cognitive Variable	Mean (sd)	Range
Working Memory		
OST (total items recalled)	15.7 (4.8)	2 – 21
SST (total items recalled)	10.3 (4.8)	1 – 20
Attentional Control		
Simon Task (ms)	99.4 (65.6)	-23.9 – 283.4
Trail Making Test (s)	36.9 (21.7)	9.1 – 106.1
Stroop Test (words)	29.0 (9.2)	11 – 55
Covariates		
WMI	105.5 (11.5)	83 – 128
PSI	112.2 (11.8)	94 – 137

OST=Operation Span Task; SST=Symmetry Span Task; FPN=Frontoparietal Network; CON=Cingulo-opercular Network.

OST and SST performance reflect total items recalled. Simon Task performance calculated by average RT of correct responses for incongruent trials – neutral trials. Trail Making performance calculated by RT for Test B – RT for Test A. Stroop Test performance calculated by number of words read in Color page – number of words read in Color-Word page.

Table 2A. Bivariate correlations between working memory and attentional control measures and within network functional connectivity

Cognitive Variable	FPN Connectivity	CON Connectivity
Working Memory		
OST	*r* = .357, *p* = .049*	*r* = .229, *p* = .229
SST	*r* = .408, *p* = .023*	*r* = .264, *p* = .151
Attentional Control		
Simon Task	*r* = -.280, *p* = .128	*r* = -.443, *p* = .013*
Trail Making Test	*r* = -.534, *p* = .002*	*r* = -.305, *p* = .095
Stroop	*r* = .444, *p* = .012*	*r* = .280, *p* = .127

OST=Operation Span Task; SST=Symmetry Span Task; FPN=Frontoparietal Network; CON=Cingulo-opercular Network

*significant at $p<0.05$

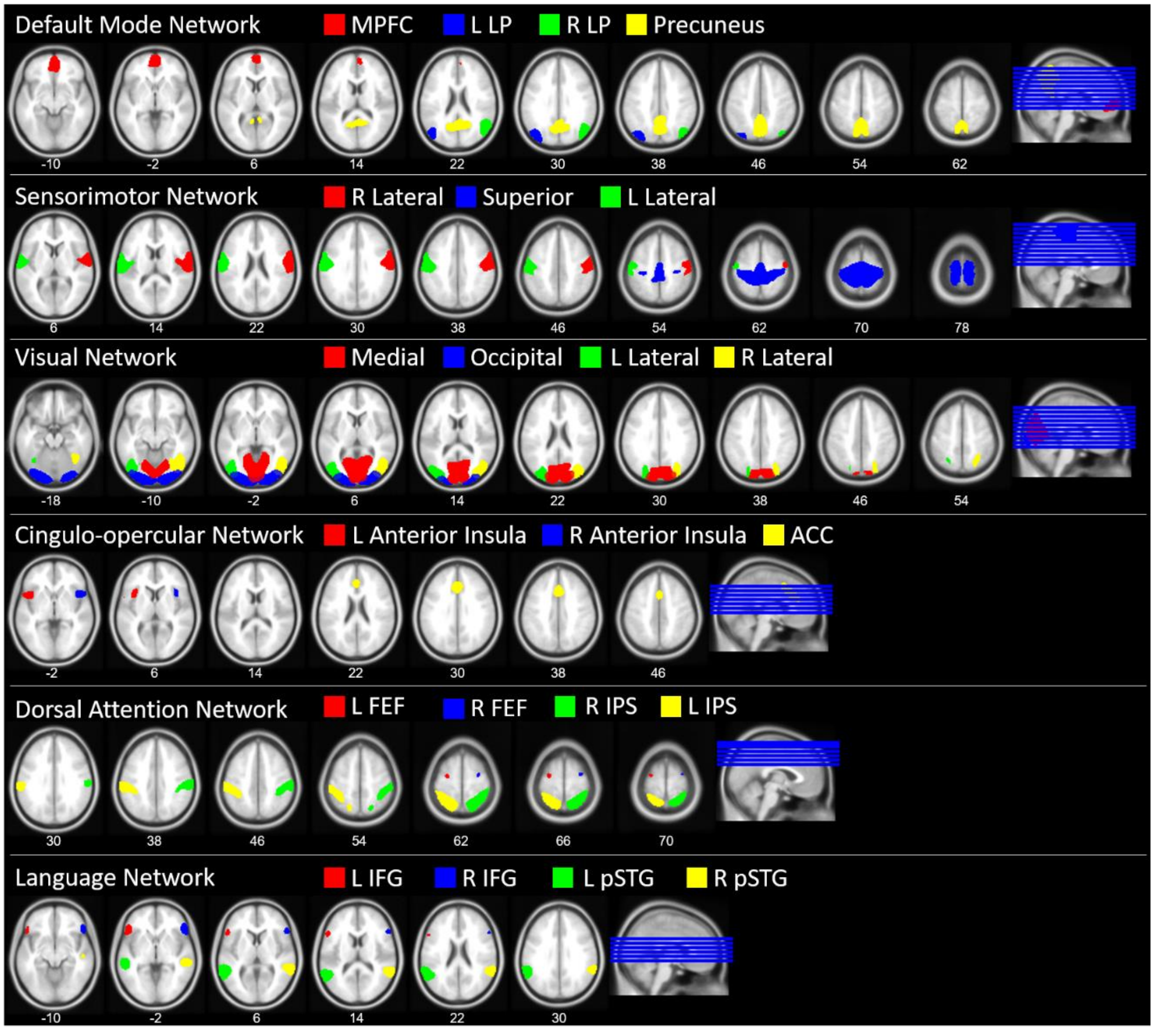

Figure A1. Overlay of each brain network and its corresponding ROIs onto a template brain. MNI Z-coordinates are displayed beneath each slice.