

Brain Volume Differences Associated With Hearing Impairment in Adults

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Abstract

Speech comprehension depends on the successful operation of a network of brain regions. Processing of degraded speech is associated with different patterns of brain activity in comparison with that of high-quality speech. In this exploratory study, we studied whether processing degraded auditory input in daily life because of hearing impairment is associated with differences in brain volume. We compared T1-weighted structural magnetic resonance images of 17 hearing-impaired (HI) adults with those of 17 normal-hearing (NH) controls using a voxel-based morphometry analysis. HI adults were individually matched with NH adults based on age and educational level. Gray and white matter brain volumes were compared between the groups by region-of-interest analyses in structures associated with speech processing, and by whole-brain analyses. The results suggest increased gray matter volume in the right angular gyrus and decreased white matter volume in the left fusiform gyrus in HI listeners as compared with NH ones. In the HI group, there was a significant correlation between hearing acuity and cluster volume of the gray matter cluster in the right angular gyrus. This correlation supports the link between partial hearing loss and altered brain volume. The alterations in volume may reflect the operation of compensatory mechanisms that are related to decoding meaning from degraded auditory input.

Keywords

hearing loss, structural plasticity, gray matter, white matter, angular gyrus, voxel-based morphometry

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Introduction

Brain plasticity following early-onset deafness is well documented (see Glick & Sharma, 2017; Merabet & Pascual-Leone, 2010 for reviews). In individuals with complete hearing loss, cortical brain areas that are normally responsible for processing auditory input, such as the primary auditory cortex (Heschl's gyrus) and the secondary auditory cortex (planum temporale), are taken over by the remaining intact senses. These areas then respond to visual, tactile, and sign-language input (Glick & Sharma, 2017). Particularly, regions in the superior temporal cortex that process auditory speech input in normal-hearing (NH) individuals respond to visual speech input in deaf individuals (Merabet & Pascual-Leone, 2010). Alterations in the brain that underlie the adaptive strategies used by individuals with *partial* hearing loss to understand speech are less studied.

One way of studying the processing of speech in hearing-impaired (HI) listeners is to assume that it bears

resemblance to the processing of degraded speech by normally hearing listeners. Speech comprehension in

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NH adults is thought to rely on a hierarchically organized network of brain regions that minimally includes bilateral superior and middle temporal gyri, the left prefrontal and premotor cortex, and the left inferior temporal cortex (Hickok and Poeppel, 2007; Peelle, Johnrude, & Davis, 2010; Rauschecker, 2011). The processing of degraded speech by NH individuals has been linked to increased activity in bilateral superior temporal cortices (Binder, Liebenthal, Possing, Medler, & Ward, 2004; Davis, Ford, Kherif, & Johnsrude, 2011; Scott, Rosen, Wickham, & Wise, 2004; Wong, Uppunda, Parrish, & Dhar, 2008; Zekveld, Heslenfeld, Festen, & Schoonhoven, 2006). Attempts to understand speech in low signal-to-noise conditions has shown to evoke activity in bilateral anterior insulae and in the opercular part of the left inferior frontal gyrus (Adank, Davis, & Hagoort, 2012; Binder et al., 2004; Zekveld et al., 2006). These areas are thought to be engaged in effortful, articulatory strategies that support the comprehension of severely distorted speech. Similarly, the premotor area and bilateral anterior superior temporal sulci, which are known to be involved in speech production, are recruited during the correct perception of distorted speech (Adank, 2012). Lastly, bilateral angular gyri and left supplementary motor area are associated with listening to distorted speech in an effortful manner (Kuchinsky et al., 2011; Wild et al., 2012). These findings raise the possibility that HI listeners may differentially recruit regions in the inferior frontal, temporal, or parietal areas while listening to speech.

A number of studies have explored functional plasticity following hearing impairment (see Mudar & Husain, 2016 for a review). In elderly listeners, hearing impairment has been linked to decreased processing in the bilateral superior temporal gyri, thalamus, and brainstem during the comprehension of linguistically complex sentences (Peelle, Troiani, Grossman, & Wingfield, 2011). In addition, altered processing has been reported in the default mode and dorsal saliency networks of HI participants in comparison with age-matched controls (Husain, Carpenter-Thompson, & Schmidt, 2014). These studies support the idea that hearing impairment may be related to altered functional processing beyond the primary auditory areas, such as the attentional, emotional, and cognitive control networks.

Studies exploring structural neuroplasticity following mild to moderate hearing loss have mostly focused on middle-aged to elderly populations (see Cardin, 2016; Mudar & Husain, 2016 for reviews). Among elderly people, hearing impairment has been associated with reduced gray matter volume in the primary auditory cortex (Husain et al., 2011; Peelle et al., 2011) and accelerated rates of gray matter volume decline in the right temporal lobe (Lin et al., 2014). Particularly, hearing loss in the higher frequency range has been shown to be

associated with gray matter volume in the left auditory cortex (Eckert, Cute, Vaden, Kuchinsky, & Dubno, 2012). In contrast, hearing impairment in middle-aged adults has been linked to increased gray matter volume in the secondary auditory cortex (Brodmann area 22; Boyen, Langers, De Kleine, & Van Dijk, 2013). In addition, changes in the integrity of white matter tracts in pathways leading to the auditory cortex, including the lateral lemniscus and the anterior thalamic radiation have been reported (Chang et al., 2004; Husain et al., 2011; Lin et al., 2008). In sum, these studies mostly point to altered gray matter volume in the superior temporal cortices, and altered white matter integrity below the primary auditory areas (although, see Profant et al., 2014); however, the extent to which the reported alterations can be attributed to hearing impairment alone is difficult to determine because of the lack of age-matched and NH or HI and younger control groups.

Studies in the domain of language and audition suggest that structural plasticity is often observed within the same brain regions that functionally underlie the behavior at hand (see Golestani, 2014, for a review). Therefore, a reasonable hypothesis would be that partial hearing loss is accompanied by gray and white matter volume alterations in the brain regions that are involved in the comprehension of degraded speech. In this study, we explored the relationship between brain volume and partial hearing loss. For this, we compared the magnetic resonance images of HI adults with those of age- and educational-level matched NH controls in a voxel-based morphometry (VBM) analysis. We hypothesized that hearing impairment would be associated with alterations in gray and white matter volume in bilateral superior temporal sulci, bilateral superior and middle temporal gyri, the left inferior frontal gyrus, the left precentral gyrus, insula, angular gyri, and the premotor area, and that these alterations would be correlated with the severity and duration of the participants' hearing impairment.

Method

Participants

In total, 17 adults with NH (5 men, 12 women; age range: 20–62, $M = 45.88$, $SD = 15.56$ years) and 17 adults with hearing impairment (5 men, 12 women; age range: 20–63, $M = 45.65$, $SD = 15.66$ years) participated in the study. HI participants were individually matched with NH ones based on age and educational level. Of the 17 pairs, 14 were individually matched based on sex, and the ratio of sex was matched between the groups.

Participants with NH were recruited from among the employees and students of the VU University medical center (VUMc) and the VU University Amsterdam, the

Netherlands. They had pure-tone thresholds of maximal 20 dB HL at the octave frequencies between 500 and 4000 Hz. The mean pure-tone average (PTA; mean hearing-threshold at 1000, 2000, and 4000 Hz, averaged over both ears) of the participants with normal hearing was 5.5 dB HL ($SD=5.5$, range: -5 to 18.3 dB HL). Thresholds at 8000 Hz were on average 17.94 dB HL ($SD=16.45$, range: -2.5 to 45 dB HL; see Figure 1 for the average hearing thresholds at the octave frequencies between 250 and 8000 Hz).

Participants with hearing impairment were recruited from among the patients of the outpatient clinic of the Ear & Hearing section of the Department of Otolaryngology-Head and Neck Surgery of the VUmc. All participants with hearing impairment had symmetrical sensorineural hearing loss. For inclusion in the current study, the mean PTA of each ear had to be between 35 and 65 dB HL. Also, the asymmetry in the pure-tone thresholds between both ears had to be at most 20 dB at one, 15 dB at two, or 10 dB at three of the octave frequencies between 250 and 4000 Hz. The mean PTA of the group with hearing impairment was 49.8 dB HL ($SD=7.3$, range: 40–61.6 dB HL). Thresholds at 8000 Hz were on average 50.88 dB HL ($SD=22.32$, range: 12.5–97.5 dB HL). The etiologies of the impairments included combinations of congenital, familial, noise-induced, and age-related hearing loss. One participant reported perinatal asphyxia as the suspected etiology, and four participants reported unknown causes. The average duration of hearing impairment was 17 years (range: 1–43 years, $SD=12$ years). Duration and

severity of hearing impairment did not correlate significantly ($r=0.42$, $p=.09$). Neither duration nor severity correlated significantly with age ($r=-0.46$, $p=.06$; $r=-0.19$, $p=.46$, respectively).

All air-bone gaps were smaller than 10 dB and all participants had normal tympanograms. All participants scored better than 80% on each ear on a speech audiogram with standard monosyllabic Dutch consonant–vowel–consonant word lists (Bosman and Smoorenburg, 1995). Furthermore, all participants were native Dutch speakers who used only spoken language and no sign language. All were classified as right-handed by the Dutch “Classification of left and right-handed subjects” (van Strien, 1992). They had normal or corrected-to-normal vision, and were screened by a near-vision test that is equivalent to the visual acuity Snellen chart (Bailey and Lovie, 1980). Exclusion criteria were the use of psychotropic medication, a history of a neurological/psychiatric disease, reading problems (e.g., dyslexia), claustrophobia, epilepsy, pregnancy, or metal in the body contraindicating MRI scanning. All participants provided written informed consent, and the study was approved by the Ethics Committee of VUmc.

MRI Acquisition

T1-weighted MRI images were obtained using a 3T GE Signa scanner (General Electric Company, Fairfield, CT, USA), equipped with an eight-channel phased array head coil, using a fast spoiled gradient-recalled echo sequence, with the following parameters: repetition time = 8,236 ms, echo time = 3.248 ms, inversion time = 450 ms, flip angle = 12° , field of view = 220 mm^2 , 166 sagittal slices, resolution = $1 \text{ mm} \times 0.9 \text{ mm} \times 0.9 \text{ mm}$.

Voxel-Based Morphometry Analysis

Image preprocessing was performed using Statistical Parametric Mapping 8 (SPM8; <http://www.fil.ion.ucl.ac.uk/spm>, Wellcome Department of Cognitive Neurology, London, UK, 2008) and VBM8-toolbox (<http://dbm.neuro.uni-jena.de/vbm.html>) that ran on Mathworks Matrix Laboratory 8.0 (MATLAB; MathWorks, Natick, MA, USA). The VBM8-toolbox was used in default settings. To reduce between-subject variability, structural images were oriented to the anterior/posterior commissure line. Thereafter, they were bias-corrected with a cutoff of 30 mm full-width-at-half-maximum and segmented into gray matter, white matter, and cerebrospinal fluid. White and gray matter images were warped to a standard stereotactic space (152 T1 MNI template, Montreal Neurological Institute) using linear affine transformation and high-dimensional DARTEL normalization (Ashburner & Friston, 2000). In this step, the normalized images were modulated using

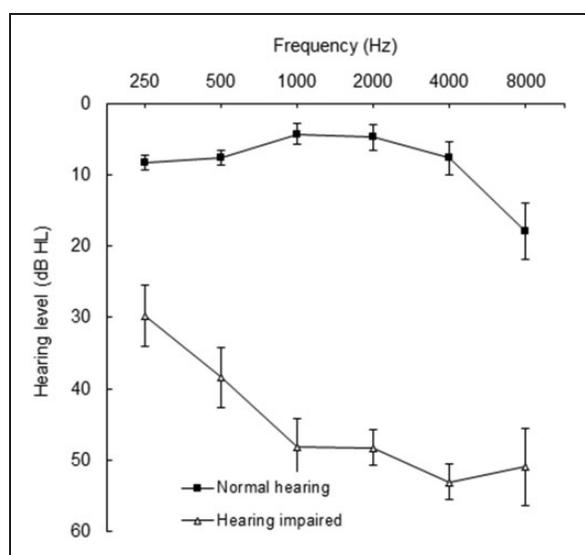


Figure 1. Pure-tone hearing thresholds (averaged over both ears) of hearing-impaired and normal-hearing participants at the octave frequencies between 250 and 8000 Hz. Error bars denote the standard error of the mean.

Table 1. Clusters That Differed in Gray or White Matter Volume Between Hearing-Impaired and Normal-Hearing Participants Revealed by the Whole-Brain Analyses.

| Contrast | L/R | Tissue | Anatomical region (Brodmann area) | k_e | T | Z | p_{uncorr} | MNI (x, y, z) |
|----------|-----|--------|--------------------------------------|-------|------|------|---------------------|---------------|
| NH < HI | R | GM | Angular gyrus (39/40) | 76 | 4.67 | 4.01 | <.001 | 36, -57, 36 |
| NH > HI | L | WM | Fusiform gyrus (19/37) | 28 | 4.13 | 3.65 | <.001 | -38, -76, -11 |

k_e = cluster size; R = right hemisphere; L = left hemisphere; GM = gray matter; WM = white matter; HI = hearing-impaired; NH = normal-hearing; MNI (x, y, z) = Montreal Neurological Institute stereotactic space coordinates.

nonlinear deformation. This is a correction for individual differences in brain size that enables the comparison of brain volume rather than tissue density (Ashburner, 2007). All images were visually inspected for quality. Covariances between the volumes were calculated to identify outliers. Finally, volumes were spatially smoothed with a 10-mm full-width-half-maximum Gaussian kernel.

To investigate differences between HI and NH adults in gray and white matter volume, we constructed general linear models (GLMs) separately for white and gray matter images using SPM 8. In these models, group (HI or NH) was the independent variable, and gray (or white) matter volume was the dependent variable. Total gray (or white) matter volume and age were included in the models as nuisance covariates. To restrict our analyses to the brain regions that are thought to be involved in listening to degraded speech, we selected the bilateral pars orbitalis, pars triangularis, pars opercularis, superior temporal gyri, Heschl's gyri, supplementary motor area, and angular gyri as regions-of-interests (ROIs). We used the Automated Anatomical Labeling (AAL) atlas (Tzourio-Mazoyer et al., 2002) to define these regions. In addition, we exclusively selected and separately considered (cf. Peelle et al., 2011) the primary auditory cortices using the bilateral TE1.0 and TE1.1 masks (Morosan et al., 2001) within the SPM Anatomy Toolbox (Eickhoff et al., 2005). Analyses for each ROI were separately conducted with a statistical threshold of $p < .05$, family-wise error rate (FWE) corrected. Last, exploratory whole-brain analyses were conducted at a more lenient threshold of $p < .001$, uncorrected, with an extent threshold of $k_e > 25$. The rationale for these whole-brain analyses was to explore hearing status-related volume changes in regions outside of the a priori hypothesized ones. The results of these analyses may be utilized in future studies (e.g., meta-analyses) that focus on related research questions.

Correlation Analyses

In order to assess the link between hearing impairment and cluster volume, we extracted the estimated gray or white matter volumes within the clusters that

significantly differed between the groups using MarsBaR (<http://marsbar.sourceforge.net>). Among the HI group, we calculated correlations between cluster volume (adjusted for total gray or white matter volume), duration of hearing impairment (in years), and hearing acuity (mean PTA in dB HL).

Results

ROI Analyses

The GLMs revealed larger gray matter volume in the right angular gyrus in the participants with hearing impairment as compared with the participants with normal hearing: $p_{\text{FWE}} < 0.05$; $T = 4.58$; $Z = 3.96$; $k_e = 52$; $MNI(x,y,z) = 36, -57, 36$. We observed no statistically significant ($p_{\text{FWE}} < 0.05$) differences in gray or white matter volume between the groups in the other predefined regions.

Whole-Brain Analyses

The GLMs revealed a cluster in the right angular gyrus with larger gray matter volume in HI listeners in comparison with NH listeners (see Figure 2 and Table 1). The coordinates of the peak voxel of this cluster were the same as those of the cluster resulting from the ROI analysis; however, this cluster was larger and exceeded the boundaries of the AAL mask. In addition, the models revealed that the participants with hearing impairment had smaller white matter volume in a cluster in the left fusiform gyrus compared with the participants with NH (see Figure 3 and Table 1).

Relationship Between Volume, Hearing Acuity, and Hearing Impairment Duration

Among the HI participants, gray matter cluster volume in the right angular gyrus (adjusted for total gray matter volume) correlated positively with severity of hearing impairment (Pearson's $r = 0.5$, $p = .04$; Figure 2c). There was no significant association between this volume and duration of hearing impairment (Pearson's $r = 0.45$, $p = .07$). White matter cluster volume in the left

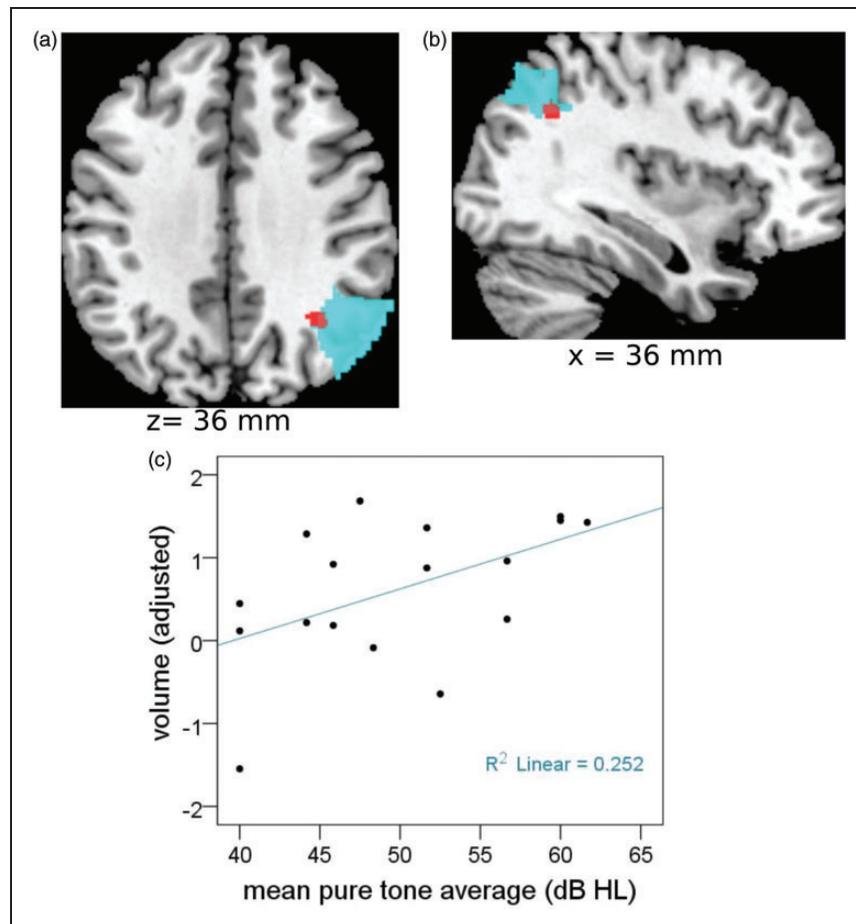


Figure 2. (a) Cluster of gray matter volume (in red) in the right angular gyrus that is larger in the hearing-impaired group as compared with the listeners with normal hearing, overlaid on the Automated Anatomical Labeling right angular gyrus mask (in blue). (b) Same region as in Figure 2(a), sagittal view. x and z are the slice coordinates in MNI space. (c) Relationship between gray matter cluster volume in the right angular gyrus and hearing acuity (mean pure-tone average at 1000, 2000, and 4000 Hz averaged over both ears) in the hearing-impaired group. Plotted are standardized gray matter residuals, adjusted for the effects of total gray matter volume.

fusiform gyrus was not statistically significantly associated with either hearing acuity or duration of hearing impairment (Pearson's $r = 0.11$, $p = .66$; Pearson's $r = 0.1$, $p = .69$, respectively).

Discussion

In this study, we explored the association between partial hearing loss and brain volume. The comparison between structural magnetic resonance images of HI and NH adults in gray and white matter volume in the areas involved in speech perception revealed larger gray matter volume in the right angular gyrus in HI listeners as compared with the NH ones. Furthermore, among the HI listeners, we observed a positive relationship between severity of hearing impairment and gray matter volume in the right angular gyrus. This relationship supports the association between altered brain volume and partial hearing loss.

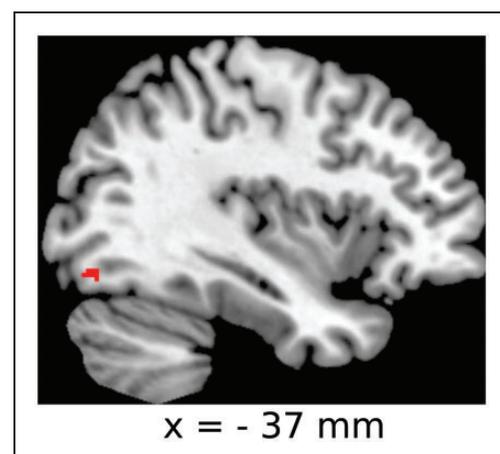


Figure 3. Cluster of white matter volume in the left fusiform gyrus that is smaller in the hearing-impaired listeners as compared with the normal-hearing ones. x is the slice coordinate in MNI space.

The angular gyrus is considered to be an interface for the integration and transfer of information from different modalities and processing subsystems (see Seghier, 2013 for a review). Studies on structural plasticity suggest that volume increases in the angular gyrus are associated with learning a new skill that requires the employment of multiple modalities (see Draganski & May, 2008 for a review). Functional neuroimaging studies with NH adults suggest the involvement of the angular gyrus in the adaptation to degraded speech (Guediche, Blumstein, Fiez, & Holt, 2014), and learning of new speech sounds (Golestani & Zattore, 2004). In the light of the above, our results may reflect mechanisms related to learning to understand distorted speech.

Differences in angular gyrus volume may also reflect the compensatory use of brain networks. Hearing impairment not only results in less sound input, but is also associated with temporal and frequency distortions that reduce the fidelity of the signal (Plomp, 1978). These distortions cannot be compensated for by hearing aids (Plomp, 1978). Functional neuroimaging studies suggest that hearing impairment may be associated with increased use of cognitive control and attentional networks that operate in concert with the angular gyrus (see Cardin, 2016 for a review). Moreover, activity in the right angular gyrus has previously been associated with the comprehension of degraded speech in the presence of visual speech cues (e.g., facial cues and lip movements; McGettigan et al., 2012). Thus, increased volume in this area may be related to the larger dependency of HI listeners on visual speech cues (Erber, 1975; Pelson & Prather, 1974). Last, larger volume in the right angular gyrus is in line with the report of increased and possibly compensatory activity in the right-hemisphere networks when listening to degraded speech (Liikkanen et al., 2007).

In addition to larger gray matter volume in the angular gyrus, our whole-brain analysis revealed smaller white matter volume in the left fusiform gyrus of the HI listeners as compared with that of the NH ones. This result goes together with reports of altered white matter integrity in the inferior fronto-occipital fasciculus in HI populations (Husain et al., 2011). However, the altered white matter volume in the fusiform gyrus should be interpreted with caution because it results from a statistically uncorrected multiple-comparison analysis that runs the risk of showing false positives.

Previous (VBM) studies with HI participants report smaller gray matter volume in the primary auditory area (Eckert et al., 2012; Peelle et al., 2011) and altered white matter volume beneath the primary auditory area (Mudar & Husain, 2016). The current comparison of HI adults with age- and educational-level matched NH listeners did not reveal any relationship between hearing impairment and brain volume in either the primary

auditory area or the white matter underneath it. This outcome supports the idea that hearing impairment alone may not be sufficient for reduced volume in the auditory cortex (Profant et al., 2014). The discrepancy between the current findings and the previous reports may be related to the complex interaction between aging and hearing loss (Wayne & Johnsrude, 2015). Whereas previous studies have focused on age-related hearing loss in mostly middle-aged to older adults (see Mudar & Husain, 2016 for a review), our participants comprised adults with variable etiologies of impairment. Because aging is associated with impaired functional connectivity in the salience network, and impaired connectivity between the salience and auditory networks (Onoda, Ishihara, & Yamaguchi, 2012), older adults with hearing impairment may perhaps benefit from adaptive strategies less compared with younger adults with hearing impairment. For this reason, decreased gray matter volume in the primary auditory cortex may be more evident in aging populations; increased gray matter volume in the right angular gyrus may be evident in individuals who benefit sufficiently from compensatory mechanisms.

The relatively small sample in the current study might have lowered the statistical sensitivity of the analyses to detect additional differences between the groups. This may particularly be the case for the left Heschl's gyrus, as this region is known to have high macro-anatomical variability between individuals (Marie et al., 2015). Furthermore, the heterogeneity in the etiologies of the hearing impairments in our sample may have limited the ability of our analyses to detect additional anatomical correlates of partial hearing loss. This study examined gray and white matter volume associated with partial hearing loss in a cross-sectional design. Although it is plausible that impaired sensory information may have led to alterations in brain volume, longitudinal studies with larger groups of moderately HI adults are needed to confirm this interpretation.

In conclusion, in this exploratory study, we investigated gray and white matter volume differences between HI and NH listeners in a VBM analysis. We observed larger gray matter volume in the right angular gyrus in the HI group as compared to the NH group. Supporting the link between volume and hearing ability, there was an association between poorer hearing acuity and larger right angular gyrus cluster volume. Together, these results suggest that residual hearing impairment may be associated with volumetric changes in higher order brain regions that are involved decoding meaning from degraded speech input.

Declaration of Conflicting Interests

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References

- Adank, P. (2012). The neural bases of difficult speech comprehension and speech production: Two activation likelihood estimation (ALE) meta-analyses. *Brain and Language*, *122*(1), 42–54. doi: 10.1016/j.bandl.2012.04.014.
- Adank, P., Davis, M. H., & Hagoort, P. (2012). Neural dissociation in processing noise and accent in spoken language comprehension. *Neuropsychologia*, *50*(1), 77–84. doi: 10.1016/j.neuropsychologia.2011.10.024.
- Ashburner, J. (2007). A fast diffeomorphic image registration algorithm. *Neuroimage*, *38*, 95–113. doi: 10.1016/j.neuroimage.2007.07.007.
- Ashburner, J., & Friston, K. J. (2000). Voxel-based morphometry—The methods. *Neuroimage*, *11*, 805–821. doi: 10.1006/nimg.2000.0582.
- Bailey, I. L., & Lovie, J. E. (1980). The design and use of a new near-vision chart. *American Journal of Optometry and Physiological Optics*, *57*(6), 378–387.
- Binder, J. R., Liebenthal, E., Possing, E. T., Medler, D. A., & Ward, B. D. (2004). Neural correlates of sensory and decision processes in auditory object identification. *Nature Neuroscience*, *7*(3), 295–301. doi: 10.1038/nrn1198.
- Bosman, A. J., & Smoorenburg, G. F. (1995). Intelligibility of Dutch CVC syllables and sentences for listeners with normal hearing and with three types of hearing impairment. *International Journal of Audiology*, *34*(5), 260–284.
- Boyen, K., Langers, D. R., de Kleine, E., & van Dijk, P. (2013). Gray matter in the brain: Differences associated with tinnitus and hearing loss. *Hearing Research*, *295*, 67–78. doi: 10.1016/j.heares.2012.02.010.
- Cardin, V. (2016). Effects of aging and adult-onset hearing loss on cortical auditory regions. *Frontiers in Neuroscience*, *10*, 199. doi: 10.3389/fnins.2016.00199.
- Chang, Y., Lee, S. H., Lee, Y. J., Hwang, M. J., Bae, S. J., Kim, M. N., ... Kang, D. S. (2004). Auditory neural pathway evaluation on sensorineural hearing loss using diffusion tensor imaging. *Neuroreport*, *15*(11), 1699–1703. doi: 10.1097/01.wnr.0000134584.10207.1a.
- Davis, M. H., Ford, M. A., Kherif, F., & Johnsrude, I. S. (2011). Does semantic context benefit speech understanding through “top-down” processes? Evidence from time-resolved sparse fMRI. *Journal of Cognitive Neuroscience*, *23*(12), 3914–3932. doi: 10.1162/jocn_a_00084.
- Draganski, B., & May, A. (2008). Training-induced structural changes in the adult human brain. *Behavioural Brain Research*, *192*(1), 137–142. doi: 10.1016/j.bbr.2008.02.015.
- Eckert, M. A., Cute, S. L., Vaden, K. I., Kuchinsky, S. E., & Dubno, J. R. (2012). Auditory cortex signs of age-related hearing loss. *Journal of the Association for Research in Otolaryngology*, *13*(5), 703–713. doi: 10.1007/s10162-012-0332-5.
- Eickhoff, S. B., Stephan, K. E., Mohlberg, H., Grefkes, C., Fink, G. R., Amunts, K., ... Zilles, K. (2005). A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *Neuroimage*, *25*(4), 1325–1335. doi: 10.1016/j.neuroimage.2004.12.034.
- Erber, N. P. (1975). Auditory-visual perception of speech. *Journal of Speech and Hearing Disorders*, *40*(4), 481–492. doi: 10.1044/jshd.4004.481.
- Glick, H., & Sharma, A. (2017). Cross-modal plasticity in developmental and age-related hearing loss: Clinical implications. *Hearing Research*, *343*, 191–201. doi: 10.1016/j.heares.2016.08.012.
- Golestani, N. (2014). Brain structural correlates of individual differences at low-to high-levels of the language processing hierarchy: A review of new approaches to imaging research. *International Journal of Bilingualism*, *18*(1), 6–34. doi: 10.1177/1367006912456585.
- Golestani, N., & Zatorre, R. J. (2004). Learning new sounds of speech: Reallocation of neural substrates. *Neuroimage*, *21*(2), 494–506. doi: 10.1016/j.neuroimage.2003.09.071.
- Guediche, S., Blumstein, S., Fiez, J., & Holt, L. L. (2014). Speech perception under adverse conditions: Insights from behavioral, computational, and neuroscience research. *Frontiers in Systems Neuroscience*, *7*, 126. doi: 10.3389/fnsys.2013.00126.
- Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience*, *8*(5), 393–402. doi: 10.1038/nrn2113.
- Husain, F. T., Carpenter-Thompson, J. R., & Schmidt, S. A. (2014). The effect of mild-to-moderate hearing loss on auditory and emotion processing networks. *Frontiers in Systems Neuroscience*, *8*, 10. doi: 10.3389/fnsys.2014.00010.
- Husain, F. T., Medina, R. E., Davis, C. W., Szymko-Bennett, Y., Simonyan, K., Pajor, N. M., ... Horwitz, B. (2011). Neuroanatomical changes due to hearing loss and chronic tinnitus: A combined VBM and DTI study. *Brain Research*, *1369*, 74–88. doi: 10.1016/j.brainres.2010.10.095.
- Kuchinsky, S. E., Vaden, K. I., Keren, N. I., Harris, K. C., Ahlstrom, J. B., Dubno, J. R., ... Eckert, M. A. (2011). Word intelligibility and age predict visual cortex activity during word listening. *Cerebral Cortex*, *22*(6), 1360–1371. doi: 10.1093/cercor/bhr211.
- Liikkanen, L. A., Tiitinen, H., Alku, P., Leino, S., Yrttiaho, S., & May, P. J. (2007). The right-hemispheric auditory cortex in humans is sensitive to degraded speech sounds. *Neuroreport*, *18*(6), 601–605. doi: 10.1097/WNR.0b013e3280b07bde.
- Lin, F. R., Ferrucci, L., An, Y., Goh, J. O., Doshi, J., Metter, E. J., ... Resnick, S. M. (2014). Association of hearing impairment with brain volume changes in older adults. *Neuroimage*, *90*, 84–92. doi: 10.1016/j.neuroimage.2013.12.059.
- Lin, Y., Wang, J., Wu, C., Wai, Y., Yu, J., & Ng, S. (2008). Diffusion tensor imaging of the auditory pathway in sensorineural hearing loss: Changes in radial diffusivity and diffusion anisotropy. *Journal of Magnetic Resonance Imaging*, *28*(3), 598–603. doi: 10.1002/jmri.21464.

- Marie, D., Jobard, G., Crivello, F., Perchey, G., Petit, L., Mellet, E., ... Tzourio-Mazoyer, N. (2015). Descriptive anatomy of Heschl's gyri in 430 healthy volunteers, including 198 left-handers. *Brain Structure and Function*, *220*(2), 729–743. doi: 10.1007/s00429-013-0680-x.
- McGettigan, C., Faulkner, A., Altarelli, I., Obleser, J., Baverstock, H., & Scott, S. K. (2012). Speech comprehension aided by multiple modalities: Behavioural and neural interactions. *Neuropsychologia*, *50*(5), 762–776. doi: 10.1016/j.neuropsychologia.2012.01.010.
- Merabet, L. B., & Pascual-Leone, A. (2010). Neural reorganization following sensory loss: The opportunity of change. *Nature Reviews Neuroscience*, *11*(1), 44–52. doi: 10.1038/nrn2758.
- Morosan, P., Rademacher, J., Schleicher, A., Amunts, K., Schormann, T., & Zilles, K. (2001). Human primary auditory cortex: Cytoarchitectonic subdivisions and mapping into a spatial reference system. *Neuroimage*, *13*(4), 684–701. doi: 10.1006/nimg.2000.0715.
- Mudar, R. A., & Husain, F. T. (2016). Neural alterations in acquired age-related hearing loss. *Frontiers in Psychology*, *7*, 828. doi: 10.3389/fpsyg.2016.00828.
- Onoda, K., Ishihara, M., & Yamaguchi, S. (2012). Decreased functional connectivity by aging is associated with cognitive decline. *Journal of Cognitive Neuroscience*, *24*(11), 2186–2198. doi: 10.1162/jocn_a_00269.
- Peelle, J. E., Johnsrude, I. S., & Davis, M. H. (2010). Hierarchical processing for speech in human auditory cortex and beyond. *Frontiers in Human Neuroscience*, *4*, 51. doi: 10.3389/fnhum.2010.00051.
- Peelle, J. E., Troiani, V., Grossman, M., & Wingfield, A. (2011). Hearing loss in older adults affects neural systems supporting speech comprehension. *The Journal of Neuroscience*, *31*(35), 12638–12643. doi: 10.1523/JNEUROSCI.2559-11.2011.
- Pelson, R. O., & Prather, W. F. (1974). Effects of visual message-related cues, age, and hearing impairment on speechreading performance. *Journal of Speech, Language, and Hearing Research*, *17*(3), 518–525. doi: 10.1044/jshr.1703.518.
- Plomp, R. (1978). Auditory handicap of hearing impairment and the limited benefit of hearing aids. *The Journal of the Acoustical Society of America*, *63*(2), 533–549.
- Profant, O., Škoch, A., Balogová, Z., Tintěra, J., Hlinka, J., & Syka, J. (2014). Diffusion tensor imaging and MR morphometry of the central auditory pathway and auditory cortex in aging. *Neuroscience*, *260*, 87–97. doi: 10.1016/j.neuroscience.2013.12.010.
- Rauschecker, J. P. (2011). An expanded role for the dorsal auditory pathway in sensorimotor control and integration. *Hearing Research*, *271*(1), 16–25. doi: 10.1016/j.heares.2010.09.001.
- Scott, S. K., Rosen, S., Wickham, L., & Wise, R. J. (2004). A positron emission tomography study of the neural basis of informational and energetic masking effects in speech perception. *Journal of the Acoustical Society of America*, *115*(2), 813–821. doi: 10.1121/1.1639336.
- Seghier, M. L. (2013). The angular gyrus multiple functions and multiple subdivisions. *The Neuroscientist*, *19*(1), 43–61. doi: 10.1177/1073858412440596.
- Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., ... Joliot, M. (2002). Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *Neuroimage*, *15*(1), 273–289. doi: 10.1006/nimg.2001.0978.
- van Strien, J. W. (1992). Classificatie van links- en rechtshandige proefpersonen [Classification of left- and right-handed subjects.]. *Nederlands Tijdschrift voor de Psychologie*, *47*, 88–92.
- Wayne, R. V., & Johnsrude, I. S. (2015). A review of causal mechanisms underlying the link between age-related hearing loss and cognitive decline. *Ageing Research Reviews*, *23*, 154–166. doi: 10.1016/j.arr.2015.06.002.
- Wild, C. J., Yusuf, A., Wilson, D. E., Peelle, J. E., Davis, M. H., & Johnsrude, I. S. (2012). Effortful listening: The processing of degraded speech depends critically on attention. *The Journal of Neuroscience*, *32*(40), 14010–14021. doi: 10.1523/JNEUROSCI.1528-12.2012.
- Wong, P. C., Uppunda, A. K., Parrish, T. B., & Dhar, S. (2008). Cortical mechanisms of speech perception in noise. *Journal of Speech, Language, and Hearing Research*, *51*(4), 1026–1041. doi: 10.1044/1092-4388(2008/075).
- Zekveld, A. A., Heslenfeld, D. J., Festen, J. M., & Schoonhoven, R. (2006). Top-down and bottom-up processes in speech comprehension. *NeuroImage*, *32*(4), 1826–1836. doi: 10.1016/j.neuroimage.2006.04.199.