The effect of hearing loss on age-related differences in neural distinctiveness

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Abstract

Age differences in cognitive performance have been shown to be overestimated if age-related hearing loss is not taken into account. Here, we investigated the role of age-related hearing loss on age differences in functional brain organization by assessing its impact on previously reported age differences in neural differentiation. To this end, we analyzed the data of 36 younger adults, 21 older adults with clinically normal hearing, and 21 older adults with mild-to-moderate hearing loss who had taken part in a functional localizer task comprising visual (i.e., faces, scenes) and auditory stimuli (i.e., voices, music) while undergoing functional magnetic resonance imaging. Evidence for reduced neural distinctiveness in the auditory cortex was observed only in older adults with hearing loss relative to younger adults, whereas evidence for reduced neural distinctiveness in the visual cortex was observed both in older adults with normal hearing and in older adults with hearing loss relative to younger adults. These results indicate that age-related dedifferentiation in the auditory cortex is exacerbated by age-related hearing loss.

Keywords: aging, age-related hearing loss, neural dedifferentiation, visual cortex, auditory cortex

Introduction

Aging has long been shown to be associated with reduced neural differentiation, particularly within the ventral visual cortex (for recent reviews, see Koen & Rugg, 2019; Koen et al., 2020). For example, studies using univariate analysis approaches have revealed that occipitotemporal regions that are specialized in processing certain visual stimulus categories (e.g., faces, scenes) show reduced neural selectivity in older adults as compared to younger adults (Koen et al., 2019; D. C. Park et al., 2004; J. Park et al., 2010, 2012; Payer et al., 2006; Srokova et al., 2020; Voss et al., 2008; Zebrowitz et al., 2016). Studies using multivariate analysis approaches have replicated and extended these findings, by showing that cortical response patterns elicited by different visual stimulus categories become less distinctive with age (e.g., Carp, Park, Polk, et al., 2011; Chamberlain et al., 2021; Koen et al., 2019; J. Park et al., 2010; Simmonite & Polk, 2022; Srokova et al., 2020). Although the vast majority of studies have focused on visually responsive regions, similar findings have been reported in the motor (Cassady et al., 2020; Carp, Park, Hebrank, et al., 2011; see also Simmonite & Polk, 2022) and auditory cortices (Lalwani et al., 2019; see also Simmonite & Polk, 2022), suggesting that age-related dedifferentiation extends across sensory and motor cortical systems.

Age-related reductions in the distinctiveness of neural representations have been proposed to be an important determinant of age-related cognitive decline (Li & Rieckmann, 2014; Li & Sikström, 2002; Li et al., 2001). Consistent with this possibility, J. Park et al. (2010) found that neural

selectivity in the ventral visual cortex significantly predicted performance on a number of cognitive tasks examining fluid processing abilities (e.g., digit symbol substitution test, trail making test, verbal fluency) in a sample of older adults (see also Koen et al., 2019). Furthermore, whereas age alone explained ~1% of the variance in a composite measure of fluid processing ability, adding neural selectivity explained an additional ~31% of the variance in fluid processing ability (J. Park et al., 2010). Similarly, a significant positive correlation between neural selectivity in the ventral visual cortex and performance on subsequent recognition memory tests has been recently shown in some studies (Koen et al., 2019; Srokova et al., 2020; see also Berron et al., 2018). Interestingly, these correlations are not only observed in older adults but also in younger adults (Koen et al., 2019; Srokova et al., 2020; but see Berron et al., 2018), suggesting that differences in neural selectivity within the ventral visual cortex may predict differences in cognitive performance regardless of age.

Importantly, a number of studies have provided evidence for greater cognitive decline among older adults with age-related hearing loss (for recent reviews, see e.g. Griffiths et al., 2020; Slade et al., 2020). Accordingly, meta-analyses have shown that age-related hearing loss is associated with poorer performance in several cognitive domains, including processing speed, memory, and executive functions (Loughrey et al., 2018; Taljaard et al., 2015), as well as with poorer global cognitive function and increased risk of dementia (Ford et al., 2018; Loughrey et al., 2018; Wei et al., 2017; Yuan et al., 2018; Zheng et al., 2017). Moreover, the association

between hearing loss and cognitive decline in older adults has been shown to result in an overestimation of *age-related* declines in different cognitive domains, such as processing speed, working memory, and inhibitory control (Guerreiro & Van Gerven, 2017).

Given the greater cognitive decline that is typically observed among older adults with hearing loss (e.g., Loughrey et al., 2018; Taljaard et al., 2015) – as well as the proposed role of reduced distinctiveness of neural representations on cognitive decline among older adults (Li & Rieckmann, 2014; Li & Sikström, 2002) –, the goal of the present study was to investigate the effect of age-related hearing loss on previously reported age differences in neural differentiation. To this end, we reanalyzed the data of two existing studies (Guerreiro et al., 2015; Rienäcker et al., 2022) to examine neural distinctiveness within visual and auditory regions in a group of younger adults, a group of older adults with normal hearing, and a group of older adults with age-related hearing loss. We hypothesized that older adults with age-related hearing loss – who typically experience greater cognitive decline (e.g., Loughrey et al., 2018; Taljaard et al., 2015) – would evince even greater reductions in neural distinctiveness relative to younger adults than those exhibited by older adults with normal hearing.

Materials and Methods

Participants

Participants were 40 younger adults (aged 20-29 years, $M = 23.7$, $SD = 2.7$, 30 women and 10 men) and 45 older adults (aged 60-83 years, $M = 66.7$, $SD = 5.1$, 18 women and 27 men), who had taken part in two research studies investigating age-related differences in the neural bases of selective attention (Guerreiro et al., 2015; Rienäcker et al., 2022)[1]. Three younger adults were excluded from data analysis because their functional localizer runs were prematurely aborted. In addition, one younger adult and three older adults were excluded due to excessive head motion (i.e., > 3 mm/°). The final sample therefore comprised 36 younger adults (aged 20-29 years, $M = 23.7$, $SD = 2.8$, 27 women and 9 men) and 42 older adults (aged 60-83 years, $M = 66.6$, $SD = 5.1$, 16 women and 26 men). All participants were right-handed and reported normal or corrected-to-normal vision. Furthermore, older participants were generally free of significant cognitive impairment, with a score of 18 or greater in the Dutch Cognitive Screening Test (De Graaf & Deelman, 1991) or with a score of 22 or greater in the Montreal Cognitive Assessment (Nasreddine et al., 2005) (for further details, see below).

In order to investigate the effect of age-related hearing loss on age differences in neural distinctiveness, the older sample was split into two groups based on their hearing sensitivity (see also Guerreiro & Van Gerven, 2017), which was assessed by measuring pure-tone detection thresholds (in dB HL) in each ear at 0.5, 1, 2, and 4 kHz with a Voyager 522 audiometer

[1] The data of these two studies were combined here because the same functional localizer task was used prior to the main experimental runs in each of these studies, in order to localize category-selective regions of interest (ROIs) in the visual and auditory cortex of each participant.

(Madsen Electronics, Taastrup, Denmark) in a sound-attenuated room. Overall hearing sensitivity was expressed as the average hearing thresholds at 1, 2, and 4 kHz for the better ear, according to recommendations for the assessment of hearing loss (Davis, 1995). In keeping with the criterion used in other brain imaging studies investigating the effect of age-related hearing loss on brain organization – according to which hearing loss has been defined as a pure-tone average greater than 25 dB HL (e.g., Campbell & Sharma, 2014; Lin et al., 2014; Luan et al., 2019; Mudar & Husain, 2016; see also Erb & Obleser, 2013; Peelle et al., 2011) –, we used a cutoff of 25 dB HL for splitting the older sample. This yielded a group of 21 older adults (aged 60-75 years, 9 women and 12 men) with clinically normal hearing (M = 17.0 dB HL, SD = 6.3) and a group of 21 older adults (aged 60-83 years, 7 women and 14 men) with mild-to-moderate hearing loss (M = 34.1 dB HL, SD = 5.7). Younger adults had clinically normal hearing (M = 7.5 dB HL, SD = 4.8). Importantly, Fisher's exact tests revealed no significant association between participant group and study [$\chi^2(2) = 0.06$, $p = 1.000$], such that the distribution of participants across the three groups did not differ between the two studies (i.e., ~50% of participants in each group originated from each study; see **Supplementary Table 1** and **Supplementary Table 2**).

Older adults with poor hearing were significantly older (M = 68.3 years, SD = 5.3) than older adults with good hearing (M = 64.9 years, SD = 4.2) [$t(40) = 2.31$, $p = .026$, $d = 0.71$]. However, the two groups did not significantly differ with regard to general cognitive function [study 1: $t(18) = 0.43$, $p = .673$, $d = -0.19$; study 2: $t(20) = 0.10$, $p = .919$, $d = 0.04$], which

was measured with the Dutch Cognitive Screening Test (De Graaf & Deelman, 1991) in the first study (older adults with good hearing: $M = 19.5$, $SD = 0.7$; older adults with poor hearing: $M = 19.4$, $SD = 0.8$) and with the Montreal Cognitive Assessment (Nasreddine et al., 2005) in the second study (older adults with good hearing: $M = 25.6$, $SD = 1.9$; older adults with poor hearing: $M = 25.7$, $SD = 2.2$).

The two studies were approved by the local ethics committee of the Maastricht Brain Imaging Center and, in accordance with the Declaration of Helsinki, informed consent was obtained from each participant prior to testing.

Experimental Procedure

The functional localizer task was presented prior to the main experimental runs in each of the two studies using E-Prime (Psychology Software Tools, Pittsburgh, PA). Four categories of stimuli were used: faces, scenes, voices, and music (for details, see Guerreiro et al., 2015). In short, visual stimuli consisted of grayscale images of male and female faces (i.e., face stimuli) and grayscale images of natural scenes (i.e., scene stimuli), whereas auditory stimuli consisted of trisyllabic, low-frequency Portuguese words (i.e., voice stimuli) and three-note melodies (i.e., music stimuli). In order to ensure that participants processed the voice stimuli phonologically (rather than semantically), only participants who had no knowledge of Portuguese were recruited. Voice stimuli were spoken by two female and two male native Portuguese speakers, whereas music stimuli were played by

one of four musical instruments (i.e., flute, guitar, marimba, and piano). Each stimulus category was presented in five 16-s blocks (during which 16 800-ms stimuli, each followed by a 200-ms inter-stimulus interval, were presented), interleaved with 16-s rest blocks[2]. The order of the blocks was counterbalanced across participants using a Latin square design. Participants were asked to passively view and hear all stimuli.

Before testing, the intensity of the auditory stimuli was individually adjusted to comfort level. This was done by increasing or decreasing the intensity of the auditory stimuli until a hearing level was reached that was both audible and comfortable for each participant.

MRI Acquisition

Data from the first study (Guerreiro et al., 2015) were acquired on a 3 T Siemens Allegra MR system (Siemens, Erlangen, Germany), equipped with a standard quadrature head coil, at the Maastricht Brain Imaging Center. Functional T2*-weighted images were acquired with an echo-planar imaging (EPI) sequence (repetition time [TR] = 2000 ms; echo time [TE] = 30 ms; flip angle [FA] = 90°; 32 axial slices; slice thickness = 3.5 mm; field of view [FOV] = 224 × 224; in-plane matrix size = 64 × 64; interleaved acquisition in ascending order) sensitive to blood oxygenation level-dependent (BOLD) contrast. Anatomical T1-weighted images were acquired with a

[2] In the second study (Rienäcker et al., 2022), each stimulus category was presented in five 18-s blocks, interleaved with 16-s rest blocks. Note that this timing difference should not affect the results because we use the β values derived from fitting a general linear model (GLM) to each participant's data. Nevertheless, we take eventual differences between the two studies into account by explicitly incorporating Study as a factor in the statistical analyses (see below).

magnetization prepared rapid gradient echo (MP-RAGE) sequence (TR = 2250 ms; TE = 2.6 ms; FA = 9°; 192 sagittal slices; voxel dimensions = 1 × 1 × 1 mm^3; FOV = 256 × 256).

Data from the second study (Rienäcker et al., 2022) were subsequently acquired on a 3 T Siemens Magnetom Prisma MR system (Siemens, Erlangen, Germany), equipped with a 64-channel head coil, at the Maastricht Brain Imaging Center. Functional T2*-weighted images were collected with an EPI sequence (TR = 2000 ms; TE = 30 ms; FA = 77°; 30 axial slices; slice thickness = 3 mm; FOV = 216 × 216; in-plane matrix size = 72 × 72; interleaved acquisition in ascending order) sensitive to BOLD contrast. Anatomical T1-weighted images were acquired with an MP-RAGE sequence (TR = 2250 ms; TE = 2.21 ms; FA = 9°; 192 sagittal slices; voxel dimensions = 1 × 1 × 1 mm^3; FOV = 256 × 256).

Visual stimuli were projected onto a rear-projection screen at the end of the scanner bore and viewed using a mirror attached to the head coil. Auditory stimuli were presented using the S14 Insert Earphones for fMRI research (Sensimetrics Corporation, Malden, MA). Foam cushions and padding were used to stabilize head position.

MRI Preprocessing

Functional and anatomical data were preprocessed using using BrainVoyager 20.6 and analyzed using BrainVoyager 22.2 (BrainInnovation, Maastricht, the Netherlands). After excluding the first two volumes, functional data underwent default preprocessing, which included slice scan

time correction, head motion correction, and removal of linear and non-linear trends above 0.005 Hz. After preprocessing, functional data were co-registered to the anatomical volume and normalized to Montreal Neurological Institute (MNI) space, resulting in an interpolated functional voxel size of 3 × 3 × 3 mm. These MNI-normalized, functional images were spatially smoothed using a Gaussian kernel of 6 mm full-width at half-maximum.

ROI Definition

In line with previous studies (Chamberlain et al., 2021; Lalwani et al., 2019), we created participant-specific ROIs based on a combination of anatomical and functional criteria. First, we restricted analyses to anatomical regions deemed to be relevant for each sensory modality, after importing the Desikan-Killiany Atlas (Desikan et al., 2006; https://identifiers.org/neurovault.image:23262) to BrainVoyager. For auditory processing, the anatomical mask contained the bilateral superior temporal gyrus, bank of the superior temporal sulcus, transverse temporal gyrus, and supramarginal gyrus (Lalwani et al., 2019). For visual processing, the anatomical mask contained the bilateral fusiform gyrus and the bilateral parahippocampal gyrus (Chamberlain et al., 2021).

Subsequently, we created participant-specific functional ROIs within these anatomical masks based on cortical responses to each experimental condition, in order to ensure that only task-relevant voxels were analyzed (see Chamberlain et al., 2021; Lalwani et al., 2019). Cortical responses (i.e.,

β values) were estimated in each voxel using a GLM that included four predictors of interest, one for each stimulus category (voices, music, faces, scenes), convolved with a canonical, two-gamma hemodynamic response function. In addition, the six translation and rotation parameters obtained by rigid body head motion correction were *z*-transformed and included as confound predictors. Finally, rest blocks were implicitly modeled as baseline in the design. Contrasts were then specified for each experimental condition (relative to baseline) and used to create auditory and visual ROIs for each participant.

The auditory ROI was created by selecting the most responsive voxels to both auditory conditions in an alternating order (i.e., the most responsive voxel to voices, followed by the most responsive voxel to music, followed by the next most responsive voxel to voices, and so on). Conversely, the visual ROI was created by selecting the most responsive voxels to both visual conditions in an alternating order (i.e., the most responsive voxel to faces, followed by the most responsive voxel to scenes, followed by the next most responsive voxel to faces, and so on). If the next most responsive voxel to a given condition had already been added to the ROI, then the next most responsive voxel that had not yet been added to the ROI was included. This process was repeated in order to create ROIs of different sizes (i.e., 1000 voxels, 2000 voxels, 5000 voxels, 10000 voxels, and entire anatomical mask; see **Figure 1** and **Figure 2**), so as to ensure that any observed effects would not depend on a specific ROI size (see also Chamberlain et al., 2021; Lalwani et al., 2019).

Neural Distinctiveness

In order to generate multiple cortical response patterns for pattern similarity analysis, we estimated cortical responses (i.e., β values) in each voxel using a GLM that included separate predictors of interest for each of the 20 task blocks (i.e., five voice blocks, five music blocks, five face blocks, and five scene blocks), convolved with a canonical, two-gamma hemodynamic response function. As before (see above), the six translation and rotation parameters obtained by rigid body head motion correction were *z*-transformed and included as confound predictors, and rest blocks were implicitly modeled as baseline in the design. Contrasts were then specified for each block of each relevant experimental condition (relative to baseline) in each ROI (see below) and used to generate cortical response patterns for each participant.

Neural distinctiveness was calculated by subtracting the similarity of cortical response patterns elicited by blocks of different experimental conditions (i.e., between-category similarity) from the similarity of cortical response patterns elicited by blocks of the same experimental condition (i.e., within-category similarity), separately by ROI and corresponding sensory modality (see Chamberlain et al., 2021; Lalwani et al., 2019). For example, during auditory processing, within-category similarity was computed in the auditory ROI as the average correlation (Fisher-transformed) in cortical response patterns between all pairs of blocks from the same auditory condition (i.e., all voice-voice pairs and all music-music pairs), whereas

between-category similarity was computed as the average correlation (Fisher-transformed) in cortical response patterns between all pairs of blocks from different auditory conditions (i.e., all voice-music pairs). Conversely, during visual processing, within-category similarity was computed in the visual ROI as the average correlation (Fisher-transformed) in cortical response patterns between all pairs of blocks from the same visual condition (i.e., all face-face pairs and all scene-scene pairs), whereas between category-similarity was computed as the average correlation (Fisher-transformed) in cortical response patterns between all pairs of blocks from different visual conditions (i.e., all face-scene pairs). A positive neural distinctiveness value indicates that cortical response patterns are more similar when elicited by the same stimulus category than when elicited by different stimulus categories, whereas a negative neural distinctiveness value would indicate that cortical response patterns are more similar when elicited by different stimulus categories than when elicited by the same stimulus category.

Neural distinctiveness values in each ROI were then submitted to a repeated measures ANOVA in IBM SPSS Statistics for Windows 28.0 (IBM Corp., Armonk, N. Y., USA), with group (3 levels: younger adults, older adults with good hearing, older adults with poor hearing) and study (2 levels: study 1, study 2) as between-group factors and ROI size (5 levels: 1000 voxels, 2000 voxels, 5000 voxels, 10000 voxels, entire anatomical mask) as a within-group factor. In these and all subsequent analyses, a Greenhouse–Geisser correction was applied to the degrees of freedom and

significance levels whenever the assumption of sphericity was violated. Planned comparisons (i.e., oneway ANOVAs) were performed separately by ROI size, in order to examine the effect of group at each level of ROI size (cf. Chamberlain et al., 2021; Lalwani et al., 2019). In these and all subsequent analyses, Welch's F was reported whenever the assumption of homogeneity of variances was violated. In the event of significant group effects, post-hoc comparisons were performed using the Games-Howell test, given its robustness when group sizes are unequal and when population variances are different. The latter analyses (i.e., oneway ANOVAs and corresponding post-hoc comparisons) were also performed as Bayesian hypothesis tests using standard priors in JASP 0.17 (JASP Team, 2023) and Bayes Factors (BF_{10}) are reported to indicate the evidential value for the alternative *vs.* null hypothesis.

Univariate Activity

In order to explore whether differences in neural distinctiveness between groups could be due to group differences in univariate activity (see also Chamberlain et al., 2021; Lalwani et al., 2019), visual cortical responses (i.e., β values) during visual processing (i.e., faces + scenes [versus baseline]) – as well as auditory cortical responses (i.e., β values) during auditory processing (i.e., voice + music [versus baseline]) – were likewise submitted to a repeated measures ANOVA, with group (3 levels: younger adults, older adults with good hearing, older adults with poor hearing) and study (2 levels: study 1, study 2) as between-group factors and ROI size (5

levels: 1000 voxels, 2000 voxels, 5000 voxels, 10000 voxels, entire anatomical mask) as a within-group factor.

Results

Neural Distinctiveness

Visual cortex. There was no effect of study [$F(1, 72) = 0.62$, $p = .434$, $\eta^2 = .01$], such that neural distinctiveness values did not significantly differ between study 1 ($M = 0.53$, $SD = 0.35$) and study 2 ($M = 0.48$, $SD = 0.25$). There was a main effect of ROI size [$F(1.32, 94.66) = 109.46$, $p < .001$, $\eta^2 = .58$], indicating that neural distinctiveness in the visual cortex decreased with increasing ROI sizes (1000 voxels: $M = 0.60$, $SD = 0.34$; 2000 voxels: $M = 0.61$, $SD = 0.31$; 5000 voxels: $M = 0.56$, $SD = 0.29$; 10000 voxels: $M = 0.42$, $SD = 0.23$; anatomical mask: $M = 0.31$, $SD = 0.19$), as well as an interaction between ROI size and study [$F(1.32, 94.66) = 3.91$, $p = .040$, $\eta^2 = .02$], such that the decrease in neural distinctiveness with increasing ROI sizes was larger in study 1 (1000 voxels: $M = 0.65$, $SD = 0.40$; 2000 voxels: $M = 0.66$, $SD = 0.37$; 5000 voxels: $M = 0.59$, $SD = 0.33$; 10000 voxels: $M = 0.43$, $SD = 0.26$; anatomical mask: $M = 0.30$, $SD = 0.21$) than in study 2 (1000 voxels: $M = 0.56$, $SD = 0.27$; 2000 voxels: $M = 0.56$, $SD = 0.24$; 5000 voxels: $M = 0.53$, $SD = 0.25$; 10000 voxels: $M = 0.42$, $SD = 0.20$; anatomical mask: $M = 0.32$, $SD = 0.17$).

Most important, there was a main effect of group [$F(2, 72) = 7.37$, $p = .001$, $\eta^2 = .17$], but no interaction between group and ROI size [$F(2.63, 94.66) = 1.10$, $p = .347$, $\eta^2 = .01$], suggesting that neural distinctiveness in the visual cortex differed significantly across groups at every ROI size (**Figure 3**, left panel). Post-hoc tests (i.e., oneway ANOVAs), performed separately by ROI size, confirmed this observation [1000 voxels: Welch's $F(2, 48.21) = 3.90$, $p = .027$, $\eta^2 = .10$, $BF_{10} = 3.12$; 2000 voxels: Welch's $F(2, 48.39) = 5.29$, $p = .008$, $\eta^2 = .13$, $BF_{10} = 8.08$; 5000 voxels: Welch's $F(2, 47.68) = 7.98$, $p = .001$, $\eta^2 = .19$, $BF_{10} = 73.45$; 10000 voxels: Welch's $F(2, 48.42) = 8.71$, $p = .001$, $\eta^2 = .20$, $BF_{10} = 108.61$; anatomical mask: Welch's $F(2, 49.16) = 9.88$, $p < .001$, $\eta^2 = .20$, $BF_{10} = 126.39$], revealing that – across ROI sizes – both older adults with good hearing [1000 voxels: $p = .026$, $d = -0.66$, $BF_{10} = 2.89$; 2000 voxels: $p = .005$, $d = -0.80$, $BF_{10} = 8.11$; 5000 voxels: $p = .001$, $d = -1.01$, $BF_{10} = 51.89$; 10000 voxels: $p < .001$, $d = -1.02$, $BF_{10} = 59.58$; anatomical mask: $p < .001$, $d = -1.05$, $BF_{10} = 77.43$] and older adults with poor hearing [1000 voxels: $p = .063$, $d = -0.62$, $BF_{10} = 1.42$; 2000 voxels: $p = .073$, $d = -0.61$, $BF_{10} = 1.32$; 5000 voxels: $p = .028$, $d = -0.72$, $BF_{10} = 2.39$; 10000 voxels: $p = .019$, $d = -0.74$, $BF_{10} = 2.74$; anatomical mask: $p = .033$, $d = -0.68$, $BF_{10} = 1.93$] tended to have lower neural distinctiveness in the visual cortex relative to younger adults. In contrast, neural distinctiveness in the visual cortex tended not to differ between older adults with good hearing and older adults with poor hearing [1000 voxels: $p = .821$, $d = 0.19$, $BF_{10} = 0.35$; 2000 voxels: $p = .407$, $d = 0.40$, $BF_{10} = 0.59$; 5000 voxels: $p = .178$, $d = 0.56$, $BF_{10} = 1.11$; 10000

voxels: $p = .133$, $d = 0.61$, $BF_{10} = 1.39$; anatomical mask: $p = .047$, $d = 0.76$, $BF_{10} = 3.15$]. Neither the Group × Study interaction [$F(2, 72) = 0.79$, $p = .459$, $\eta^2 = .02$] nor the Group × ROI Size × Study interaction [$F(2.63, 94.66) = 0.62$, $p = .585$, $\eta^2 = .01$] reached significance.

Auditory cortex. There was a main effect of study [$F(1, 72) = 9.50$, $p = .003$, $\eta^2 = .12$], indicating that neural distinctiveness values were higher in study 1 ($M = 0.48$, $SD = 0.29$) than in study 2 ($M = 0.32$, $SD = 0.22$). The main effect of ROI size was likewise significant [$F(1.33, 95.62) = 148.06$, $p < .001$, $\eta^2 = .64$], such that neural distinctiveness in the auditory cortex decreased with increasing ROI sizes (1000 voxels: $M = 0.52$, $SD = 0.31$; 2000 voxels: $M = 0.49$, $SD = 0.28$; 5000 voxels: $M = 0.43$, $SD = 0.24$; 10000 voxels: $M = 0.37$, $SD = 0.21$; anatomical mask: $M = 0.19$, $SD = 0.12$). The interaction between ROI size and study did not reach significance [$F(1.33, 95.62) = 3.12$, $p = .069$, $\eta^2 = .01$], suggesting that the decrease in neural distinctiveness with increasing ROI sizes did not significantly differ between study 1 (1000 voxels: $M = 0.62$, $SD = 0.34$; 2000 voxels: $M = 0.58$, $SD = 0.30$; 5000 voxels: $M = 0.53$, $SD = 0.25$; 10000 voxels: $M = 0.45$, $SD = 0.21$; anatomical mask: $M = 0.23$, $SD = 0.12$) and study 2 (1000 voxels: $M = 0.43$, $SD = 0.25$; 2000 voxels: $M = 0.40$, $SD = 0.22$; 5000 voxels: $M = 0.35$, $SD = 0.20$; 10000 voxels: $M = 0.30$, $SD = 0.18$; anatomical mask: $M = 0.14$, $SD = 0.11$).

Crucially, the main effect of group was significant [$F(2, 72) = 4.86$, $p = .010$, $\eta^2 = .12$], suggesting that neural distinctiveness in the auditory

cortex differed significantly across groups. This effect was, however, qualified by an interaction with ROI size [$F(2.66, 95.62) = 4.32$, $p = .009$, $\eta^2 = .04$], such that group differences in neural distinctiveness differed across ROI sizes (**Figure 3,** right panel). Post-hoc tests (i.e., oneway ANOVAs), performed separately by ROI size, revealed a main effect of group at nearly all ROI sizes except for the largest one [1000 voxels: $F(2, 75) = 4.27$, $p = .017$, $\eta^2 = .10$, $BF_{10} = 3.17$; 2000 voxels: $F(2, 75) = 4.59$, $p = .013$, $\eta^2 = .11$, $BF_{10} = 4.04$; 5000 voxels: $F(2, 75) = 4.23$, $p = .018$, $\eta^2 = .10$, $BF_{10} = 3.08$; 10000 voxels: $F(2, 75) = 3.42$, $p = .038$, $\eta^2 = .08$, $BF_{10} = 1.66$; anatomical mask: $F(2, 75) = 1.77$, $p = .177$, $\eta^2 = .05$, $BF_{10} = 0.46$], such that – across all four ROI sizes – neural distinctiveness in the auditory cortex was significantly lower in older adults with poor hearing relative to younger adults [1000 voxels: $p = .011$, $d = -0.83$, $BF_{10} = 4.74$; 2000 voxels: $p = .013$, $d = -0.83$, $BF_{10} = 2.79$; 5000 voxels: $p = .016$, $d = -0.82$, $BF_{10} = 4.45$; 10000 voxels: $p = .040$, $d = -0.74$, $BF_{10} = 2.72$], but not significantly different between older adults with good hearing and younger adults [1000 voxels: $p = .132$, $d = -0.51$, $BF_{10} = 1.15$; 2000 voxels: $p = .082$, $d = -0.57$, $BF_{10} = 0.95$; 5000 voxels: $p = .114$, $d = -0.55$, $BF_{10} = 1.39$; 10000 voxels: $p = .167$, $d = -0.50$, $BF_{10} = 1.08$] nor between older adults with good hearing and older adults with poor hearing [1000 voxels: $p = .759$, $d = -0.22$, $BF_{10} = 0.37$; 2000 voxels: $p = .876$, $d = -0.15$, $BF_{10} = 0.33$; 5000 voxels: $p = .870$, $d = -0.16$, $BF_{10} = 0.34$; 10000 voxels: $p = .906$, $d = -0.13$, $BF_{10} = 0.33$]. Neither the Group × Study interaction [$F(2, 72) = 0.79$, $p = .459$, $\eta^2 = .02$] nor the

Group × ROI Size × Study interaction [$F(2.66, 95.62) = 0.30$, $p = .801$, $\eta^2 = .00$] reached significance.

Univariate Activity

Visual cortex. There was no effect of study [$F(1, 72) = 0.30$, $p = .586$, $\eta^2 = .00$], such that visual cortical responses during visual processing did not significantly differ between study 1 ($M = 1.91$, $SD = 1.06$) and study 2 ($M = 1.79$, $SD = 0.94$). The main effect of ROI size was significant [$F(1.07, 77.12) = 508.83$, $p < .001$, $\eta^2 = .87$], indicating that visual cortical responses to visual stimuli decreased with increasing ROI sizes (1000 voxels: $M = 2.91$, $SD = 0.99$; 2000 voxels: $M = 2.42$, $SD = 0.81$; 5000 voxels: $M = 1.77$, $SD = 0.58$; 10000 voxels: $M = 1.25$, $SD = 0.41$; anatomical mask: $M = 0.90$, $SD = 0.33$). Study did not interact with this effect [$F(1.07, 77.12) = 0.50$, $p = .494$, $\eta^2 = .00$], such that the decrease in visual cortical responses to visual stimuli with increasing ROI sizes did not significantly differ between study 1 (1000 voxels: $M = 2.99$, $SD = 1.10$; 2000 voxels: $M = 2.52$, $SD = 0.90$; 5000 voxels: $M = 1.85$, $SD = 0.62$; 10000 voxels: $M = 1.29$, $SD = 0.44$; anatomical mask: $M = 0.91$, $SD = 0.35$) and study 2 (1000 voxels: $M = 2.83$, $SD = 0.89$; 2000 voxels: $M = 2.34$, $SD = 0.73$; 5000 voxels: $M = 1.70$, $SD = 0.53$; 10000 voxels: $M = 1.21$, $SD = 0.39$; anatomical mask: $M = 0.89$, $SD = 0.33$).

Importantly, neither the main effect of group [$F(2, 72) = 0.49$, $p = .614$, $\eta^2 = .01$] nor any of the interactions involving the factor group reached

significance [Group × ROI Size: $F(2.14, 77.12) = 1.17$, $p = .319$, $\eta^2 = .00$; Group × Study: $F(1, 72) = 1.04$, $p = .359$, $\eta^2 = .03$; Group × ROI Size × Study: $F(2.14, 77.12) = 1.62$, $p = .203$, $\eta^2 = .01$], revealing that visual cortical responses during visual processing did not significantly differ across groups (**Figure 4,** left panel). Planned comparisons (i.e., oneway ANOVAs), separately by ROI size, confirmed this observation [1000 voxels: $F(2, 75) = 0.69$, $p = .507$, $\eta^2 = .02$; 2000 voxels: $F(2, 75) = 0.57$, $p = .570$, $\eta^2 = .01$; 5000 voxels: $F(2, 75) = 0.35$, $p = .708$, $\eta^2 = .01$; 10000 voxels: $F(2, 75) = 0.21$, $p = .809$, $\eta^2 = .01$; anatomical mask: $F(2, 75) = 0.34$, $p = .715$, $\eta^2 = .01$].

Auditory cortex. There was a main effect of study [$F(1, 72) = 32.99$, $p < .001$, $\eta^2 = .31$], indicating that auditory cortical responses during auditory processing were significantly higher in study 1 ($M = 3.34$, $SD = 1.67$) than in study 2 ($M = 2.15$, $SD = 1.40$). The main effect of ROI size was likewise significant [$F(1.07, 77.17) = 630.07$, $p < .001$, $\eta^2 = .87$], such that auditory cortical responses to auditory stimuli decreased with increasing ROI sizes (1000 voxels: $M = 4.18$, $SD = 1.62$; 2000 voxels: $M = 3.61$, $SD = 1.39$; 5000 voxels: $M = 2.81$, $SD = 1.08$; 10000 voxels: $M = 2.18$, $SD = 0.84$; anatomical mask: $M = 0.79$, $SD = 0.38$), as was the interaction between ROI size and study [$F(1.07, 77.17) = 20.69$, $p < .001$, $\eta^2 = .03$], suggesting that the decrease in auditory cortical responses to auditory stimuli with increasing ROI sizes was more pronounced in study 1 (1000 voxels: $M = 5.07$, $SD = 1.26$; 2000 voxels: $M = 4.42$, $SD = 1.08$; 5000 voxels: $M = 3.49$,

SD = 0.81; 10000 voxels: *M* = 2.71, *SD* = 0.64; anatomical mask: *M* = 1.01, *SD* = 0.31) than in study 2 (1000 voxels: *M* = 3.37, *SD* = 1.48; 2000 voxels: *M* = 2.87, *SD* = 1.23; 5000 voxels: *M* = 2.21, *SD* = 0.91; 10000 voxels: *M* = 1.70, *SD* = 0.71; anatomical mask: *M* = 0.59, *SD* = 0.32).

Crucially, neither the main effect of group [$F(2, 72) = 1.26$, $p = .291$, $\eta^2 = .03$] nor any of the interactions involving the factor group reached significance [Group × ROI Size: $F(2.14, 77.17) = 0.80$, $p = .462$, $\eta^2 = .00$; Group × Study: $F(2, 72) = 0.56$, $p = .573$, $\eta^2 = .02$; Group × ROI Size × Study: $F(2.14, 77.17) = 0.77$, $p = .477$, $\eta^2 = .00$], revealing that auditory cortical responses during auditory processing did not significantly differ across groups (**Figure 4,** right panel). Planned comparisons (i.e., oneway ANOVAs), separately by ROI size, confirmed this observation [1000 voxels: $F(2, 75) = 0.81$, $p = .447$, $\eta^2 = .02$; 2000 voxels: $F(2, 75) = 0.81$, $p = .448$, $\eta^2 = .02$; 5000 voxels: $F(2, 75) = 0.93$, $p = .399$, $\eta^2 = .02$; 10000 voxels: $F(2, 75) = 0.96$, $p = .390$, $\eta^2 = .02$; anatomical mask: $F(2, 75) = 1.17$, $p = .316$, $\eta^2 = .03$].

Discussion

Given the proposed role of neural distinctiveness on age-related differences in cognitive performance (Li & Rieckmann, 2014; Li & Sikström, 2002; Li et al., 2001), as well as the increasingly recognized association between age-related hearing loss and cognitive decline (e.g., Loughrey et al., 2018; Taljaard et al., 2015), the goal of the present study was to investigate the impact of age-related hearing loss on previously reported

age differences in neural differentiation. To do so, we compared neural distinctiveness within the visual and auditory cortices between older adults with mild-to-moderate hearing loss, older adults with clinically normal hearing, and a control group of younger adults.

We had hypothesized that older adults with age-related hearing loss – who typically experience greater cognitive decline than older adults with normal hearing (e.g., Loughrey et al., 2018; Taljaard et al., 2015) – would exhibit greater reductions in neural distinctiveness relative to younger adults than those exhibited by older adults with normal hearing. Our results are partially consistent with this hypothesis. Indeed, we found evidence for neural dedifferentiation in the auditory cortex only when comparing older adults with poor hearing with younger adults, and not when comparing older adults with good hearing with younger adults. Note that had we disregarded age-related hearing loss and compared all older adults with the younger group, then we would have concluded – as have previous studies (Lalwani et al., 2019; Simmonite & Polk, 2022) – that older adults show reduced neural distinctiveness in the auditory cortex relative to younger adults (see **Supplementary Results**). Importantly, because in the present study older adults with poor hearing were also significantly older than older adults with good hearing (see **Methods**), the present findings could still arguably be accounted for by a true aging effect (which is only detected in an older group of older adults). In order to rule out this possibility, we repeated our analyses after matching older participants with good hearing and older participants with poor hearing based on their age (see

Supplementary Results). These additional analyses, on a smaller subset of participants, entirely replicated the present findings. That is, older adults with poor hearing – despite their now lower age range – had reduced neural distinctiveness in the auditory cortex relative to younger adults, whereas differences between older adults with good hearing and younger adults did not reach significance. Taken together, these results indicate that age-related dedifferentiation in the auditory cortex (Lalwani et al., 2019; see also Simmonite & Polk, 2022) is exacerbated by age-related hearing loss. This effect may be related to a greater decrease in auditory GABA levels among older adults with age-related hearing loss (see Gao et al., 2015; see also Dobri & Ross, 2021; but see Profant et al., 2013), as lower GABA levels have been shown to be associated with reduced neural distinctiveness in the corresponding sensory cortices (Chamberlain et al., 2021; Lalwani et al., 2019).

Neural distinctiveness in the visual cortex, on the other hand, was not only significantly reduced in older adults with poor hearing relative to younger adults, but also – and even more consistently so – in older adults with good hearing relative to younger adults. This pattern of results indicates that neural dedifferentiation in the visual cortex is not exacerbated by age-related hearing loss, and is therefore not in line with our hypothesis. In fact, we had hypothesized that older adults with poor hearing – among whom greater age-related cognitive decline has been reported (Guerreiro & Van Gerven, 2017) – would exhibit even greater reductions in neural distinctiveness relative to younger adults than those exhibited by older

adults with good hearing, an effect that should be especially noted in the ventral visual cortex, as neural dedifferentiation in this region in particular has been shown to be associated with greater cognitive decline among other adults (e.g., Koen et al., 2019; J. Park et al., 2010). The present results would therefore seem to suggest that the greater cognitive decline that is typically observed among older adults with age-related hearing loss as compared to older adults with normal hearing abilities (e.g., Loughrey et al., 2018; Taljaard et al., 2015) cannot be explained by greater neural dedifferentiation in this group. However, global cognitive function did not significantly differ between the present group of older adults with good hearing and the present group of older adults with poor hearing (see **Methods**), so this possibility cannot be definitely ruled out here. Importantly, the lack of significant differences in global cognitive function between older adults with good hearing and older adults with poor hearing in the present study is not surprising for two reasons: first, differences in global cognitive function between older adults with poor hearing and older adults with good hearing have been shown to have a small effect size (e.g., Loughrey et al., 2018), so they are more likely to be detected in studies using very large samples (e.g., Rutherford et al., 2018); second, in each of the two original studies (Guerreiro et al., 2015; Rienäcker et al., 2022) we had strived to recruit healthy, community-dwelling older adults with no evidence of significant cognitive impairment. Finally – and worth noting –, we found very little evidence for a relationship between neural distinctiveness and cognitive function in the present study (see

Supplementary Results), which is likely due to differences in measures of cognitive function across studies (cf. J. Park et al., 2010; Koen et al., 2019; Srokova et al., 2020). In contrast to the present study, in which a very limited range of cognitive tests were used (see **Supplementary Table 1** and **Supplementary Table 2**), previous studies that were explicitly aimed at investigating the relationship between neural selectivity and cognitive function have typically included a much more comprehensive and fine-grained assessment of cognitive function (see Koen et al., 2019; J. Park et al., 2010; Srokova et al., 2020).

The group differences in neural distinctiveness reported in the present study are unlikely to be due to differences in univariate activity across groups (see also Chamberlain et al., 2021; Lalwani et al., 2019). Indeed, we observed that both groups of older adults showed reduced neural distinctiveness in the visual cortex relative to younger adults, yet there were no significant group differences in univariate visual cortical responses during visual processing. Furthermore, we observed that older adults with poor hearing showed significantly reduced neural distinctiveness in the auditory cortex relative to younger adults, yet there were no significant group differences in univariate auditory cortical responses during auditory processing. Finally, a set of additional analyses in which mean univariate activity was included as a covariate (not reported) entirely replicated the group differences in neural distinctiveness reported above, further corroborating the notion that group differences in neural distinctiveness are unlikely to be explained by differences in univariate activity across groups.

Group differences in neural distinctiveness – especially those in the visual cortex – are also unlikely to be explained by differences in visual acuity across groups. First, participants in the present study did report normal or corrected-to-normal vision – although, admittedly, there were significant group differences in visual acuity (see also e.g. Koen et al., 2019; Zebrowitz et al., 2016), such that both older adults with good hearing and older adults with poor hearing had significantly lower visual acuity than younger adults (see **Supplementary Table 1** and **Supplementary Table 2**). Importantly, partial correlations across the entire sample, while controlling for chronological age, yielded no evidence for an association between neural distinctiveness in the visual cortex and measures of visual acuity in study 1 [1000 voxels: r_p = -.14, p = .427; 2000 voxels: r_p = -.11, p = .514; 5000 voxels: r_p = -.10, p = .574; 10000 voxels: r_p = -.03, p = .851; anatomical mask: r_p = -.01, p = .978] or study 2 [1000 voxels: r_p = -.11, p = .503; 2000 voxels: r_p = -.13, p = .421; 5000 voxels: r_p = -.13, p = .434; 10000 voxels: r_p = -.17, p = .299; anatomical mask: r_p = -.18, p = .263]. Second, Chamberlain et al. (2021) found evidence for age-related dedifferentiation in the visual cortex in older adults relative to younger adults even after controlling for visual acuity. Finally, visual acuity failed to mediate the relationship between age and measures of neural dedifferentiation in a study that employed mediation analyses to explicitly examine possible mediators of age-related dedifferentiation in the visual cortex (Zebrowitz et al., 2016).

Current evidence suggests that age differences in neural distinctiveness are due to both an age-related increase in the similarity of cortical response patterns elicited by different stimulus categories (i.e., between-category similarity) and an age-related decrease in the reliability of cortical response patterns elicited by identical stimulus categories (i.e., within-category similarity) (Simmonite & Polk, 2022; see also Carp, Park, Polk, et al., 2011). We therefore further explored the effect of age-related hearing loss on age differences in both of these mechanisms (see **Supplementary Results**). Across visual and auditory cortices, we found that differences in neural distinctiveness across groups were due to group differences in the reliability of cortical response patterns elicited by identical stimulus categories, rather than by group differences in the similarity of cortical response patterns elicited by different stimulus categories (see also Chamberlain et al., 2021, for similar results in the visual cortex; and Simmonite & Polk, 2022, for similar results in the auditory cortex). Specifically, both older adults with good hearing and older adults with poor hearing exhibited lower within-category similarity values in the visual cortex relative to younger adults, whereas between-category similarity values in the visual cortex did not significantly differ across groups. Furthermore, within-category similarity values in the auditory cortex tended to be lower in older adults with poor hearing relative to younger adults, but not significantly different between older adults with good hearing and younger adults, whereas between-category similarity values in the auditory cortex did not significantly differ across groups.

Simmonite and Polk (2022) have also recently provided evidence for a relationship between neural distinctiveness in different cortical regions, particularly in older adults. In the present study, we likewise found some evidence for a relationship between neural distinctiveness in the visual and auditory cortices, but only when this relationship was examined across the entire sample (see **Supplementary Results**). Moreover, as Simmonite and Polk (2022), we also found evidence for a relationship between within-category similarity values in the visual and auditory cortices, not only when this relationship was examined across the entire sample but also when it was examined separately in each group. Finally, although there was no evidence for a relationship between between-category similarity values in the visual and auditory cortices in the study by Simmonite and Polk (2022), evidence for such a relationship emerged in the present study in the group of older adults with poor hearing.

In conclusion, the results of the present study suggest that age-related hearing loss does not modulate age differences in neural distinctiveness within the ventral visual cortex. In contrast, when the effects of age-related hearing loss are minimized – by comparing younger adults and older adults with clinically normal hearing –, age differences in neural distinctiveness within the auditory cortex can no longer be reliably observed. These results demonstrate that hearing loss exacerbates age-related dedifferentiation in the auditory cortex, likely due to a greater reduction in auditory GABA levels among older adults with hearing loss (Gao et al., 2015).

Disclosure Statement

The authors report there are no competing interests to declare.

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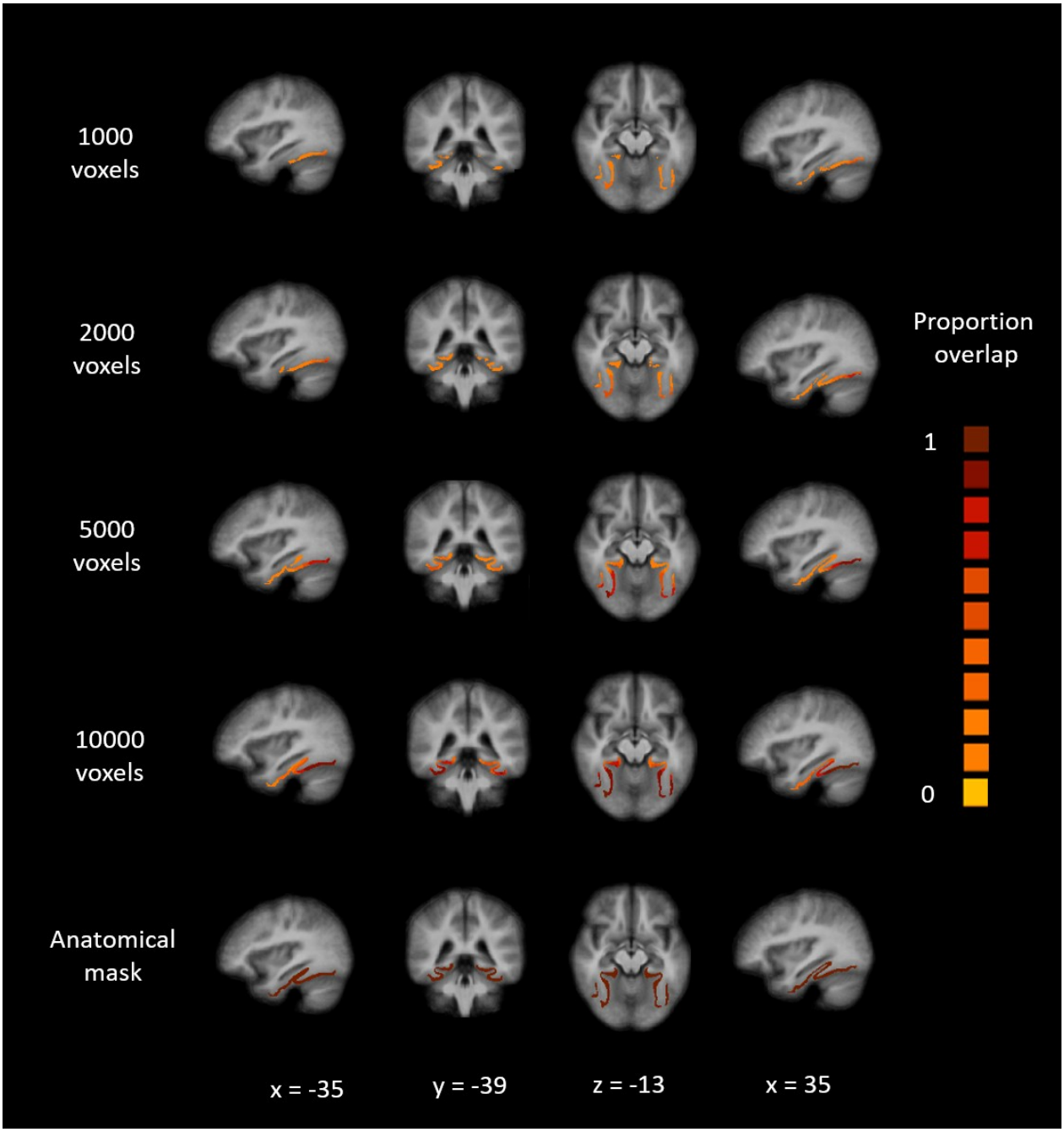

Figure 1. Probabilistic maps of the visual region of interest (ROI) as a function of ROI size, overlaid on the average normalized T1 image of all participants. Probability values range from 0 to 1, whereby 0 indicates no participant at a given voxel and 1 indicates that all participants share that voxel.

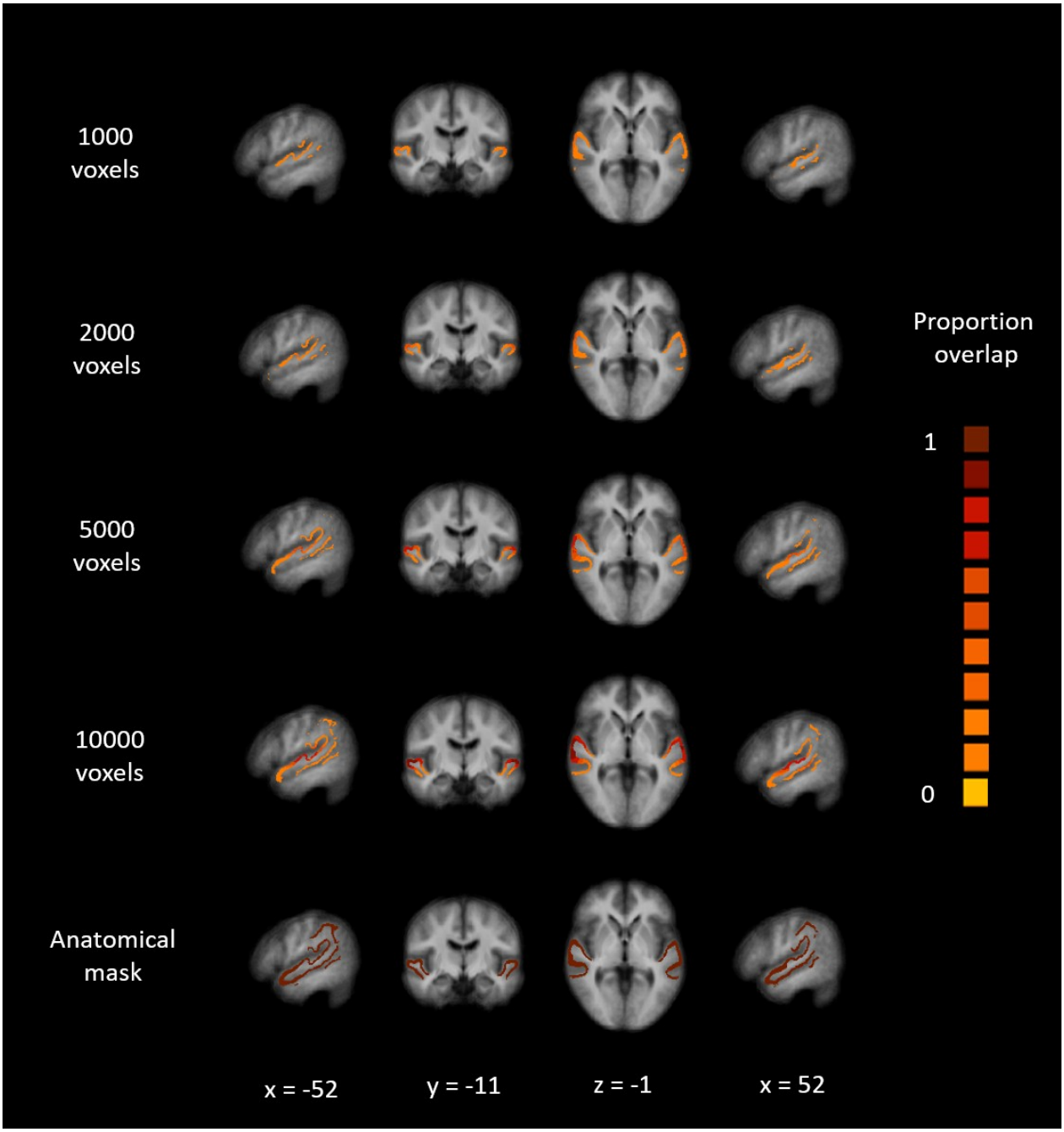

Figure 2. Probabilistic maps of the auditory region of interest (ROI) as a function of ROI size, overlaid on the average normalized T1 image of all participants. the average normalized T1 structural image of all participants. Probability values range from 0 to 1, whereby 0 indicates no participant at a given voxel and 1 indicates that all participants share that voxel.

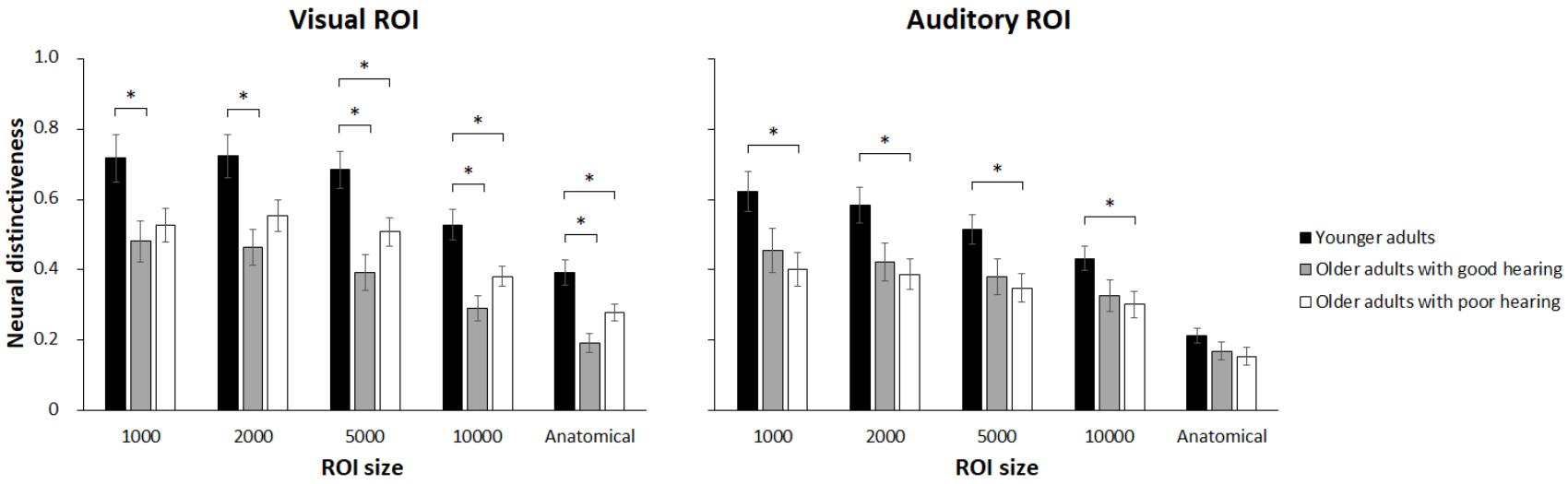

Figure 3. Mean neural distinctiveness in the visual cortex (left panel) and in the auditory cortex (right panel) as a function of ROI size and group. Younger adults are plotted in black, older adults with good hearing are plotted in grey, and older adults with poor hearing are plotted in white. Error bars represent standard errors of the mean. * $p < .050$

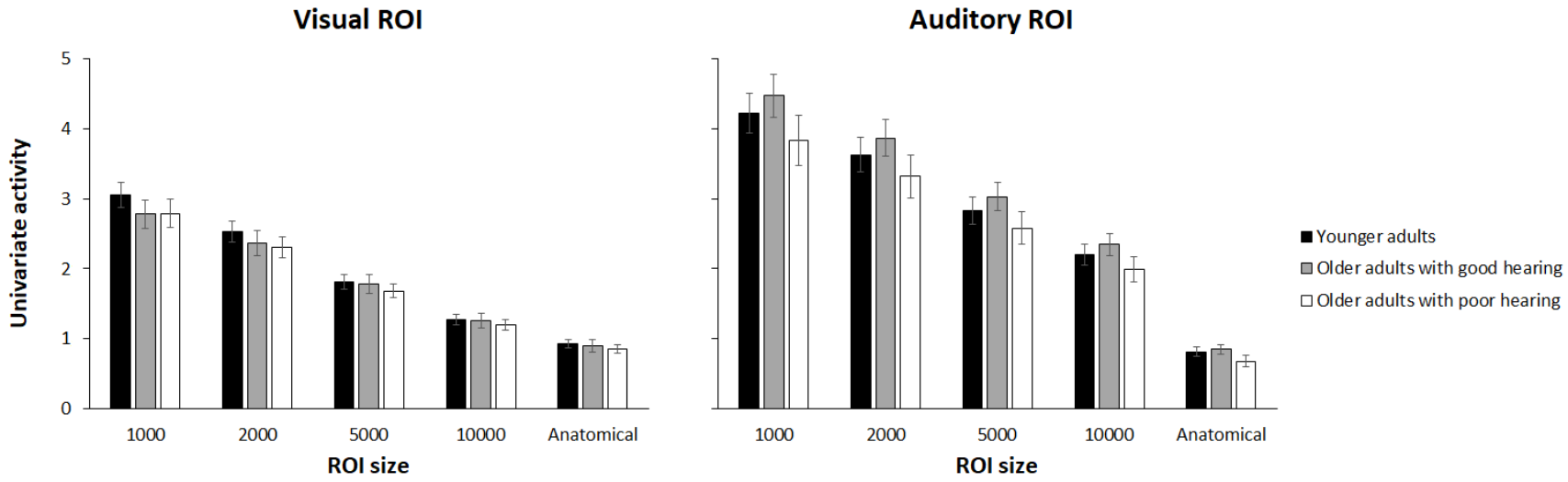

Figure 4. Mean univariate activity in the visual cortex during visual processing (left panel) and in the auditory cortex during auditory processing (right panel). Younger adults are plotted in black, older adults with good hearing are plotted in grey, and older adults with poor hearing are plotted in white. Error bars represent standard errors of the mean.